

# WENLOCK AND LUDLOW MARINE COMMUNITIES IN WALES AND THE WELSH BORDERLAND

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**ABSTRACT.** Five major marine benthonic communities, the (1) *Salopina*, (2) *Homoospira/Sphaerirhynchia*, (3) *Isorthis*, (4) *Dicoelosia*, and (5) *Visbyella* communities occupied clastic sediments laid down in areas of increasing depth from the shoreline to deep areas in Wales and the Welsh Borderland during Wenlock and Ludlow times. The communities are described statistically and are shown to be completely intergrading in composition. They are dominated by epifaunal brachiopods, and so differ markedly from modern benthonic communities which are primarily infaunal. Other minor faunal associations are described.

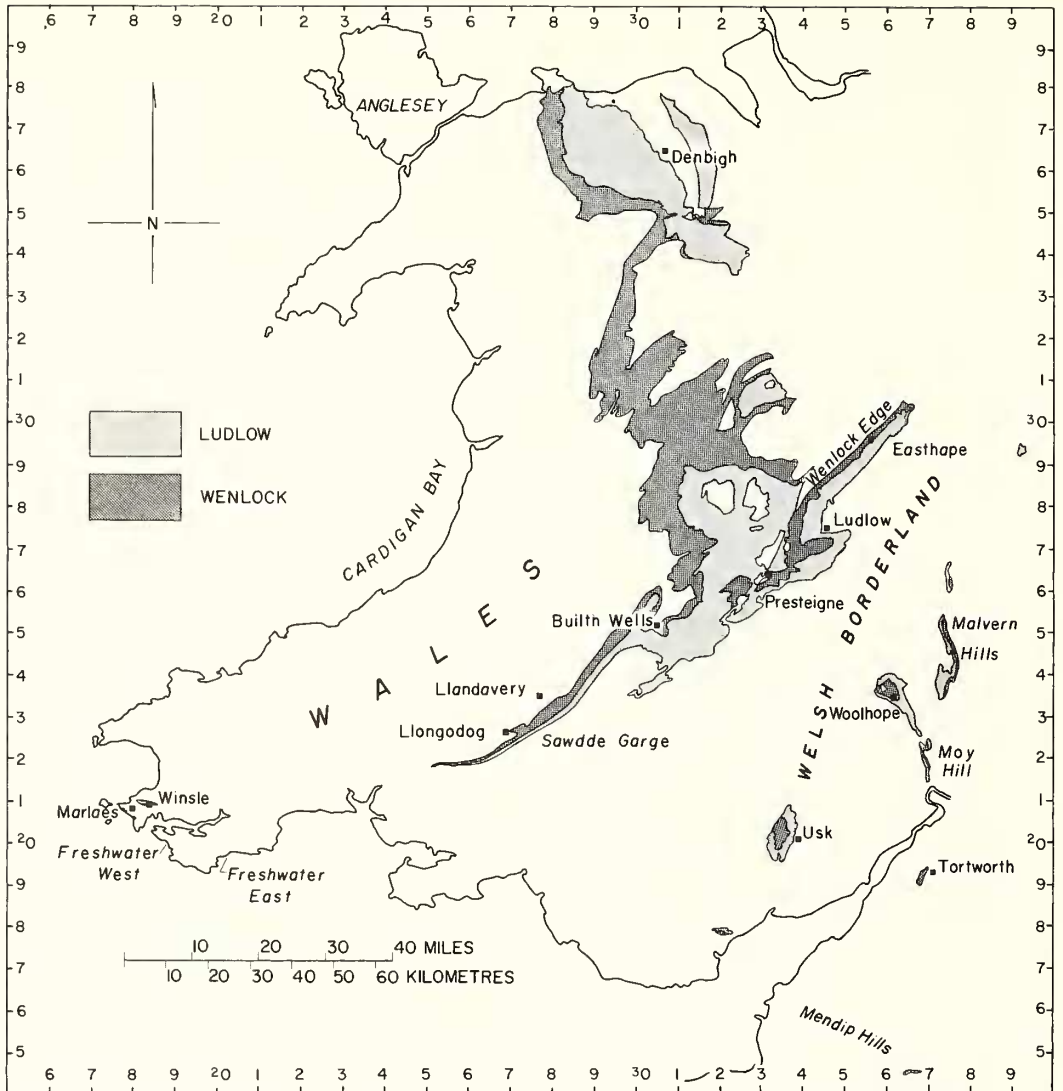
A species diversity gradient from low in the shallow-water *Salopina* community to high in the deep-water *Dicoelosia* community is analogous to modern benthonic diversity gradients. A density gradient running in the opposite sense suggests food was scarcer in deep water and thus important in determining brachiopod distribution. The *Visbyella* community probably lived at depths greater than the *Dicoelosia* community and represents the deepest limits of Silurian benthonic life.

SHELLY deposits now exposed in areas of Wales and the inliers of the Welsh Borderland (text-fig. 1) were mostly laid down during the Wenlock and Ludlow on the stable eastern margin of the Welsh basin but some faunas extended into the basin. The benthonic animals which were ultimately fossilized lived in loose associations called communities. We assume that the distribution of the animals was controlled by their tolerances to multiple environmental factors, those species with similar tolerances tending to occur together. But because no two species ever reacted in exactly the same way to the environmental complex, the communities they formed were not entities of fixed composition, but varied continuously from place to place and through time.

The recognition of ancient communities from their preserved remains (community palaeoecology) has been shown to be a productive approach to palaeoecology through the work of Craig (1954), Johnson (1962), Ziegler (1965), Bayer (1967), Bretsky (1969), and many others. Previous authors, largely neglecting the problem of describing communities in a way that expresses their inherent variability, characterized their communities merely by a list of species often divided into 'common' and 'associated' species. However, the continuously variable nature of communities means they must be described and classified in statistical terms. This paper presents such statistical descriptions of hitherto unstudied Wenlock and Ludlow communities using methods unfamiliar to palaeontologists but traditional in plant ecology. The relationship of the communities to the environments existing at the time is demonstrated. The communities studied all come from clastic sediments; some carbonates appear to contain variants of the communities which have not been considered in this paper.

## METHODS

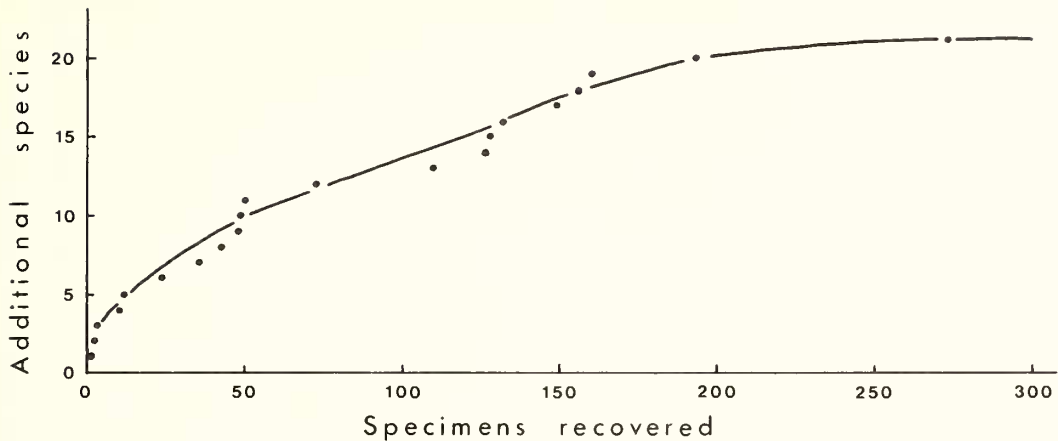
Out of 111 bulk fossil collections used in this study, 96 were collected by the authors from single beds or within 20 cm of section at the localities listed in the Appendix.



TEXT-FIG. 1. Outcrop of Wenlock and Ludlow rocks with names of collection areas.

The collections were broken up in the laboratory and all macrofossils saved. Species counts were based on the most abundant valve in each case. Nearly all the collections are large enough (usually 100–200 specimens) to reproduce the actual number of species and the proportions between them in the sampled bed. This is proved by the diminishing rate of appearance of additional species as collection size increases (text-fig. 2).

In some beds, fossils are concentrated near the base by wave or current action, but usually they are found throughout; the valves are almost always disarticulated. In cases where measurements have been carried out, we find that differently shaped



TEXT-FIG. 2. First appearance of species in collection LD-S-3 as a function of collection size.

brachial and pedicle valves of a single species have the same width, indicating a lack of hydrodynamic sorting. From such measurements and our observations of large shells occurring in fine grain sediment, we conclude that post-mortem transport capable of obscuring the community distribution and composition did not affect the collections. Furthermore, the fact that the same faunal associations are so frequently repeated suggests that the animals in each association were living in the same general area. Beds, such as turbidites, in which mixed assemblages can sometimes be recognized, are not included in this paper. It is probable that any original patches of living animals were homogenized over short distances, and that the communities are 'time-averaged' (Walker and Bambach 1971, p. 783).

On the basis of recurring species associations, most collections have been assigned to one of the following five communities: the *Salopina* community, the *Homoeospira/Sphaerirhynchia* community, the *Isorthis* community, the *Dicoelosia* community, and the *Visbyella* community. By community, we merely mean a number of species inhabiting the same local area. A fossil community is one which we know only from its members' fossilized remains. The community is defined by all the species which occur in it, and their relative abundances, not just by the one or two abundant species after which the community is named.

The statistical indices used in the community descriptions which follow are based on those of Curtis (1959, pp. 79-83) and were developed to describe vegetation. The derivation and meanings of these indices are listed in Table 1. There are three classes of indices shown in the table which describe respectively species, collection, and community characteristics. We believe the combination of all the indices gives a more complete picture of particular ancient communities than has been provided in the past, and suggest that future community work include such information.

TABLE 1. Descriptive indices, their derivations and meanings.

| NAME OF INDEX                                | MATHEMATICAL DERIVATION  | INTUITIVE MEANING               |   |   |
|--|--|---------------------------------|---|---|
|  |  | SPECIES CHARACTERISTICS         | COLLECTION CHARACTERISTICS                                  | COMMUNITY CHARACTERISTICS                       |
| PRESENCE PERCENTAGE<br>(abbreviated Pres. %) | $\frac{\text{No. of collections where species occurs}}{\text{Total no. of collections}} \times 100\%$  | Ubiquity                        | Degree of uniformity among collections within the community | Distinctness of a community from its neighbours |
| FREQUENCY PRESENCE                           | Pres. % $\times$ Average numerical abundance in collections where species occurs   | Commonness                      | Average no. of species per collection                       | Amount of similarity between two communities    |
| PREVALENT SPECIES                            | The top species in a community, ordered by presence percentage and frequency presence. The number of prevalent species is the average number of species per collection (i.e. species density); thus a diverse community (high species density) contains more prevalent species than an undiverse one | Widespread in the community     |   |   |
| FIDELITY                                     | No. of communities in which species occurs   | Ecological tolerance of species |   |   |
| MODAL COMMUNITY                              | Community where species reaches highest frequency presence   | Ecological 'acme' of species    |   |   |
| HOMOGENEITY                                  | $\frac{\text{Pres. \% of prevalent species}}{\text{Pres. \% of all species}}$  |                                 |   |   |
| SPECIES DENSITY                              | $\frac{\text{Total of nos. of species in each collection from the community}}{\text{No. of collections in the community}}$   |                                 |   |   |
| COMMUNITY DISTINCTNESS                       | $\frac{\text{No. of prevalent species modal in the community}}{\text{Total no. of prevalent species in the community}} \times 100\%$   |                                 |   |   |
| SIMILARITY COEFFICIENT                       | $2w/a+b$ . Where: $a = \Sigma$ frequency presence for all species of one community, $b = \Sigma$ equivalent value for other community, $w = \Sigma$ of lower values of frequency presence for each species   |                                 |   |   |



## THE COMMUNITIES

The five major communities are described by means of the quantitative information in Tables 2–11. The tables are based solely on the brachiopod fraction of the fauna for two reasons: (1) brachiopods generally make up at least 90% of the total fauna, (2) the taxonomic uncertainty is less with brachiopods than with most other groups. Additional information about the community, including its non-brachiopod fauna, follows each table.

TABLE 2. Composition of the Wenlock *Salopina* community.

## WENLOCK

## SALOPINA COMMUNITY

| PREVALENT SPECIES                                 | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|---|---------------------|--------------------|
| 1. <i>Salopina</i>                                | 94.1                | 1981.0             |
| 2. ' <i>Camarotoechia</i> ' <i>nucula</i>         | 88.2                | 2236.2             |
| 3. <i>A.</i> ( <i>Pembrostrophia</i> )            | 29.4                | 545.0              |
| 4. <i>Lingula</i>                                 | 29.4                | 93.9               |
| 5. <i>Rhynchotreta cuneata</i>                    | 23.5                | 173.4              |
| 6. <i>Craniops</i>                                | 23.5                | 137.1              |
| 7. <i>Leptostrophia filosa</i>                    | 23.5                | 49.2               |
| OTHER SPECIES                                     |                     |                    |
| 8. <i>Atrypa</i>                                  | 23.5                | 43.9               |
| 9. <i>Meristina</i>                               | 23.5                | 32.4               |
| 10. <i>Orbiculoidea</i>                           | 23.5                | 28.1               |
| 11. ' <i>Camarotoechia</i> ' <i>tripartita</i>    | 17.6                | 211.1              |
| 12. <i>Protochonetes</i> sp.                      | 17.6                | 180.6              |
| 13. <i>Homoeospira</i>                            | 17.6                | 121.2              |
| 14. <i>Eocoelia angelini</i>                      | 17.6                | 89.0               |
| 15. <i>Howellella</i> spp.                        | 17.6                | 88.7               |
| 16. <i>Sphaerirhynchia wilsoni</i>                | 17.6                | 38.6               |
| 17. <i>Amphistrophia</i> spp.                     | 17.6                | 37.7               |
| 18. Athyrids                                      | 17.6                | 36.9               |
| 19. <i>Whitfieldella</i>                          | 17.6                | 12.7               |
| 20. <i>Marklandella</i>                           | 11.8                | 241.7              |
| 21. <i>Strophochonetes</i>                        | 11.8                | 140.1              |
| 22. <i>Coolinia</i>                               | 11.8                | 23.0               |
| 23. Rhynchonellids                                | 11.8                | 15.9               |
| 24. <i>Mclearnites</i>                            | 5.9                 | 257.0              |
| 25. <i>Sphaerirhynchia davidsoni</i>              | 5.9                 | 173.3              |
| 26. ' <i>Camarotoechia</i> ' <i>llandoveriana</i> | 5.9                 | 26.5               |
| 27. <i>Shagamella</i>                             | 5.9                 | 21.2               |
| 28. <i>Schizotreta</i>                            | 5.9                 | 12.9               |
| 29. <i>Cordatomyonia edgelliana</i>               | 5.9                 | 9.8                |
| 30. <i>Striispirifer</i>                          | 5.9                 | 8.8                |
| 31. <i>Leptaena</i> spp.                          | 5.9                 | 5.9                |
| 32. <i>Gypidula</i>                               | 5.9                 | 4.7                |
| 33. <i>Hyattidina</i>                             | 5.9                 | 4.5                |
| 34. <i>Eospirifer</i>                             | 5.9                 | 2.9                |

Number of collections studied = 17  
Species density = 6.5

Homogeneity = 47.33%  
Distinctness coefficient = 57.1%

1. *Salopina community* (Tables 2 and 3)

Besides the brachiopod content listed in the tables, bivalves, especially *Pteronitella* and *Palaeopecten*, and the distinctive genus *Nuculites*, frequently occur. Gastropods are often present, though they are rarely abundant. *Tentaculites* is common, especially in the Wenlock.

A common feature of the *Salopina* community is the numerical dominance of a few species. For example, collection SG-15 (Ludlow of the Sawdde Gorge) contains 54% *Salopina lunata*, 24% *Howellella elegans*, and 9% *Sphaerirhynchia wilsoni*, a total of 87% for just three species.

The most important difference between Tables 2 and 3 is the enormous increase from the Wenlock to the Ludlow in *Protochonetes* (excluding *P. minimus* which is confined to deeper-water communities). The lower homogeneity in the Wenlock is attributable to locally distributed species: for example, *Amphistrophia* (*Pembrostrophia*) *freshwaterensis* appears to be confined to Pembrokeshire (Bassett 1971, pp. 325-327), and the rhynchonellid we have called '*Camarotoechia*' *tripartita* has been recorded only from the East Mendips.

TABLE 3. Composition of the Ludlow *Salopina* community.

## LUDLOW

## SALOPINA COMMUNITY

| PREVALENT SPECIES                              | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|--|---------------------|--------------------|
| 1. <i>Protochonetes ludloviensis</i>           | 100.0               | 3185.1             |
| 2. ' <i>Camarotoechia</i> ' <i>nucula</i>      | 100.0               | 1274.8             |
| 3. <i>Salopina</i>                             | 83.3                | 2456.8             |
| 4. <i>Howellella</i> spp.                      | 75.0                | 498.9              |
| 5. <i>Sphaerirhynchia wilsoni</i>              | 58.3                | 185.4              |
| 6. <i>Orbiculoidea</i>                         | 50.0                | 48.5               |
| 7. <i>Dayia</i>                                | 41.7                | 254.4              |
| OTHER SPECIES                                  |                     |                    |
| 8. <i>Lingula</i>                              | 41.7                | 47.5               |
| 9. <i>Whitfieldella</i>                        | 25.0                | 183.7              |
| 10. <i>Leptostrophia filosa</i>                | 25.0                | 121.7              |
| 11. <i>Atrypa</i>                              | 25.0                | 51.4               |
| 12. <i>Craniops</i>                            | 16.7                | 162.0              |
| 13. <i>Isorthis</i>                            | 16.7                | 70.2               |
| 14. <i>Strophochonetes</i>                     | 16.7                | 63.9               |
| 15. <i>Hyattidina</i>                          | 8.3                 | 30.3               |
| 16. <i>Schizotreta</i>                         | 8.3                 | 9.6                |
| 17. <i>Schizocrania</i>                        | 8.3                 | 9.6                |
| 18. ' <i>Camarotoechia</i> ' <i>tripartita</i> | 8.3                 | 5.0                |
| 19. <i>Leptaena</i> spp.                       | 8.3                 | 4.7                |
| 20. <i>Shaleria</i>                            | 8.3                 | 3.5                |

Number of collections studied = 12  
Species density = 7.2

Homogeneity = 69.93%  
Distinctness coefficient = 57.1%

2. *Homoeospira* or *Sphaerirhynchia* communities (Tables 4 and 5)

The faunas of the *Homoeospira* and *Sphaerirhynchia* communities are very similar. Because of this the two communities may be considered variants of one, living at different times. During the Wenlock the brachiopod *Homoeospira* is one of the dominant species. Unpublished studies by Mr. J. M. Hurst of Oxford University

TABLE 4. Composition of the Wenlock *Homoeospira* community.

## WENLOCK

*HOMOEOSPIRA* COMMUNITY

| PREVALENT SPECIES                        | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|--|---------------------|--------------------|
| 1. <i>Howellella</i> spp.                | 100.0               | 1477.1             |
| 2. ' <i>Camarotoechia</i> ' <i>nucla</i> | 90.9                | 628.7              |
| 3. <i>Salopina</i>                       | 81.8                | 444.2              |
| 4. <i>Homoeospira</i>                    | 72.7                | 1030.5             |
| 5. <i>Atrypa</i>                         | 63.6                | 1375.9             |
| 6. <i>Leptostrophia filosa</i>           | 45.5                | 197.5              |
| 7. <i>Amplustrophia</i> spp.             | 45.5                | 177.7              |
| 8. <i>Meristina</i>                      | 45.5                | 138.5              |
| 9. <i>Protochonetes</i> sp.              | 36.4                | 176.3              |
| 10. <i>Cranitops</i>                     | 36.4                | 117.5              |
| OTHER SPECIES                            |                     |                    |
| 11. <i>Leptaena</i> spp.                 | 36.4                | 108.1              |
| 12. <i>Sphaerirhynchia wilsoni</i>       | 27.3                | 69.6               |
| 13. <i>Gypidula</i>                      | 27.3                | 57.3               |
| 14. <i>Isorthis</i>                      | 27.3                | 52.7               |
| 15. <i>Dalejina</i>                      | 27.3                | 32.7               |
| 16. <i>Protochonetes minimus</i>         | 18.2                | 203.1              |
| 17. <i>Marklandella</i>                  | 18.2                | 156.3              |
| 18. <i>Rhynchotreta cuneata</i>          | 18.2                | 86.4               |
| 19. <i>Resserella canalis</i>            | 18.2                | 78.2               |
| 20. <i>Eospirifer</i>                    | 18.2                | 72.7               |
| 21. <i>Eocoeha angelini</i>              | 18.2                | 37.3               |
| 22. <i>Protomegastrophia</i>             | 18.2                | 26.4               |
| 23. <i>Nucleospira</i>                   | 18.2                | 12.7               |
| 24. <i>A.</i> ( <i>Pembrostrophia</i> )  | 9.1                 | 410.9              |
| 25. <i>Hyattidina</i>                    | 9.1                 | 67.8               |
| 26. <i>Mcleanites</i>                    | 9.1                 | 62.7               |
| 27. <i>Brachyprion</i>                   | 9.1                 | 32.0               |
| 28. <i>Striispirifer</i>                 | 9.1                 | 27.5               |
| 29. <i>Aegiria grayi</i>                 | 9.1                 | 21.8               |
| 30. <i>Whitfieldella</i>                 | 9.1                 | 21.8               |
| 31. <i>Coolinia</i>                      | 9.1                 | 16.4               |
| 32. <i>Strophochonetes</i>               | 9.1                 | 12.7               |
| 33. <i>Sphaerirhynchia davidsoni</i>     | 9.1                 | 12.5               |
| 34. Athyrids                             | 9.1                 | 4.5                |
| 35. <i>Strophonella</i>                  | 9.1                 | 3.6                |

Number of collections studied = 11  
Species density = 10.2

Homogeneity = 60.21%  
Distinctness coefficient = 40.0%

indicate that in the Wenlock Limestone (late Wenlock) *Sphaerirhynchia* has become equally important. By the Ludlow *Sphaerirhynchia* has become a dominant species with *Homoeospira* of minor significance. Text-fig. 3 shows the shift in importance.

Changes in community composition with time can have various causes, such as disappearance of a species followed by the spread of a new species into the vacant ecological niche, or the result of facies changes. The shift from *Homoeospira* to *Sphaerirhynchia* can probably be related to facies changes, *Sphaerirhynchia* preferring carbonates. In the Ludlow of Wales, *Sphaerirhynchia* predominates in both carbonates and clastics.

Pteroid bivalves are frequently present and so are the locally abundant *Fuchsella amygdalina* and *Paracyclas* sp., especially in the Ludlow.

The name *Homoeospira* community has been selected for the Wenlock despite the greater abundance of *Howellella* (Table 4) because of the wide distribution of *Howellella* (text-fig. 3) through the communities. Other abundant species ('*Camarotoechia*' *nucula* and *Salopina*) are even more abundant in the *Salopina* community.

TABLE 5. Composition of the Ludlow *Sphaerirhynchia* community.

LUDLOW

SPHAERIRHYNCHIA COMMUNITY

| PREVALENT SPECIES                         | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|---|---------------------|--------------------|
| 1. <i>Sphaerirhynchia wilsoni</i>         | 100.0               | 1442.0             |
| 2. ' <i>Camarotoechia</i> ' <i>nucula</i> | 100.0               | 1099.0             |
| 3. <i>Salopina</i>                        | 88.9                | 1106.5             |
| 4. <i>Protochonetes ludloviensis</i>      | 88.9                | 848.7              |
| 5. <i>Whitfieldella</i>                   | 77.8                | 779.1              |
| 6. <i>Isorthis</i>                        | 66.7                | 979.5              |
| 7. <i>Howellella</i> spp.                 | 55.6                | 857.6              |
| 8. <i>Dayia</i>                           | 55.6                | 309.2              |
| 9. <i>Leptostrophia filosa</i>            | 44.4                | 452.0              |
| 10. <i>Lingula</i>                        | 44.4                | 133.8              |
| OTHER SPECIES                             |                     |                    |
| 11. <i>Atrypa</i>                         | 44.4                | 131.7              |
| 12. <i>Craniops</i>                       | 33.3                | 70.9               |
| 13. <i>Mesopholidostrophia</i> spp.       | 22.2                | 72.4               |
| 14. <i>Homoeospira</i>                    | 22.2                | 45.7               |
| 15. <i>Orbiculoidea</i>                   | 22.2                | 25.7               |
| 16. <i>Shagamella</i>                     | 11.1                | 140.0              |
| 17. <i>Trigonirhynchia</i>                | 11.1                | 49.8               |
| 18. <i>Gypidula</i>                       | 11.1                | 18.7               |
| 19. <i>Leptaena</i> spp.                  | 11.1                | 12.4               |
| 20. <i>Protochonetes minimus</i>          | 11.1                | 12.2               |
| 21. <i>Strophonella</i>                   | 11.1                | 6.2                |
| 22. <i>Amphistrophia</i> spp.             | 11.1                | 6.2                |
| 23. <i>Nucleospira</i>                    | 11.1                | 6.2                |
| 24. <i>Strophochonetes</i>                | 11.1                | 4.3                |

Number of collections studied = 9  
Species density = 9.7

Homogeneity = 74.17%  
Distinctness coefficient = 40.0%

3. *Isorthis* community (Tables 6 and 7)

Bivalves and gastropods are uncommon in this community, and there are no characteristic genera. The high species density in the *Isorthis* community is part

TABLE 6. Composition of the Wenlock *Isorthis* community.

| PREVALENT SPECIES                         | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|---|---------------------|--------------------|
| 1. <i>Isorthis</i>                        | 100·0               | 957·0              |
| 2. <i>Atrypa</i>                          | 100·0               | 597·4              |
| 3. <i>Howellella</i> spp.                 | 87·5                | 388·6              |
| 4. <i>Resserella canalis</i>              | 75·0                | 638·6              |
| 5. <i>Eospirifer</i>                      | 75·0                | 386·5              |
| 6. <i>Eoplectodonta</i> spp.              | 75·0                | 366·0              |
| 7. <i>Amphistrophia</i> spp.              | 75·0                | 186·6              |
| 8. ' <i>Camarotoechia</i> ' <i>nucula</i> | 62·5                | 226·3              |
| 9. <i>Coolinia</i>                        | 50·0                | 180·6              |
| 10. <i>Craniops</i>                       | 37·5                | 638·9              |
| 11. <i>Striispirifer</i>                  | 37·5                | 319·0              |
| 12. <i>Anastrophia</i>                    | 37·5                | 140·7              |
| 13. <i>Protochonetes</i> sp.              | 37·5                | 130·4              |
| 14. <i>Leptaena</i> spp.                  | 37·5                | 122·6              |
| 15. <i>Salopina</i>                       | 37·5                | 76·6               |
| 16. <i>Gypidula</i>                       | 37·5                | 48·1               |
| OTHER SPECIES                             |                     |                    |
| 17. Orthids                               | 37·5                | 36·6               |
| 18. <i>Atrypina</i>                       | 37·5                | 27·9               |
| 19. <i>Dinobolus</i>                      | 25·0                | 543·8              |
| 20. <i>Protochonetes minimus</i>          | 25·0                | 180·4              |
| 21. <i>Meristina</i>                      | 25·0                | 156·3              |
| 22. <i>Dalejina</i>                       | 25·0                | 131·2              |
| 23. <i>Whitfieldella</i>                  | 25·0                | 106·6              |
| 24. <i>Skenidioides</i>                   | 25·0                | 85·0               |
| 25. <i>Leptostrophia filosa</i>           | 25·0                | 82·5               |
| 26. <i>Mesopholidostrophia</i> spp.       | 25·0                | 63·7               |
| 27. Athyrids                              | 25·0                | 50·0               |
| 28. <i>Leptaena</i> aff. <i>purpurea</i>  | 25·0                | 36·9               |
| 29. <i>Nucleospira</i>                    | 25·0                | 30·7               |
| 30. <i>Clorinda</i> sp.                   | 25·0                | 18·7               |
| 31. <i>Strophonella</i>                   | 25·0                | 11·2               |
| 32. <i>Cordatomyonia edgelliana</i>       | 12·5                | 104·1              |
| 33. <i>Trigonirhynchia</i>                | 12·5                | 92·5               |
| 34. <i>Cyrtia</i>                         | 12·5                | 51·2               |
| 35. <i>Sphaerirhynchia wilsoni</i>        | 12·5                | 40·0               |
| 36. <i>Leangella</i>                      | 12·5                | 23·7               |
| 37. <i>Homoeospira</i>                    | 12·5                | 23·7               |
| 38. <i>Orbiculoidea</i>                   | 12·5                | 21·2               |
| 39. <i>Eocoelia angelini</i>              | 12·5                | 21·2               |
| 40. <i>Strophochonetes</i>                | 12·5                | 19·1               |
| 41. <i>Katastrophomena</i>                | 12·5                | 13·8               |
| 42. <i>Spirigerina</i>                    | 12·5                | 12·5               |
| 43. <i>Shagamella</i>                     | 12·5                | 7·5                |



TABLE 6 (cont.):

| OTHER SPECIES                      | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|------------------------------------|---------------------|--------------------|
| 44. <i>Brachyprion</i>             | 12.5                | 7.5                |
| 45. <i>Protomegastrophia</i>       | 12.5                | 6.2                |
| 46. <i>Leptostrophia compressa</i> | 12.5                | 6.2                |
| 47. <i>Dictyonella</i>             | 12.5                | 5.0                |
| 48. <i>Lingula</i>                 | 12.5                | 5.0                |

Number of collections studied = 8  
Species density = 15.7

Homogeneity = 60.83%  
Distinctness coefficient = 50.0%

TABLE 7. Composition of the Ludlow *Isorthis* community.

## LUDLOW

## ISORTHIS COMMUNITY

| PREVALENT SPECIES                         | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|---|---------------------|--------------------|
| 1. <i>Isorthis</i>                        | 100.0               | 2567.8             |
| 2. <i>Mesopholidostrophia</i> spp.        | 71.4                | 668.1              |
| 3. <i>Sphaerirhynchia wilsoni</i>         | 64.3                | 354.5              |
| 4. <i>Atrypa</i>                          | 57.1                | 559.0              |
| 5. <i>Dalejina</i>                        | 50.0                | 1137.8             |
| 6. ' <i>Camarotoechia</i> ' <i>nucula</i> | 50.0                | 191.1              |
| 7. <i>Craniops</i>                        | 50.0                | 154.8              |
| 8. <i>Anphistrophia</i> spp.              | 50.0                | 141.4              |
| 9. <i>Shagamella</i>                      | 42.9                | 761.6              |
| 10. <i>Leptostrophia filosa</i>           | 42.9                | 321.2              |

## OTHER SPECIES

|                                       |      |       |
|---------------------------------------|------|-------|
| 11. <i>Howellella</i> spp.            | 42.9 | 232.7 |
| 12. <i>Homoeospira</i>                | 42.9 | 62.1  |
| 13. <i>Salopina</i>                   | 35.7 | 126.1 |
| 14. <i>Leptaena</i> spp.              | 35.7 | 114.1 |
| 15. <i>Coolinia</i>                   | 28.6 | 77.8  |
| 16. <i>Protochonetes minimus</i>      | 28.6 | 21.2  |
| 17. <i>Shaleria</i>                   | 21.4 | 430.6 |
| 18. <i>Strophonella</i>               | 21.4 | 106.6 |
| 19. <i>Aegiria grayi</i>              | 21.4 | 40.3  |
| 20. <i>Lingula</i>                    | 21.4 | 37.1  |
| 21. <i>Whitfieldella</i>              | 21.4 | 18.9  |
| 22. <i>Dayia</i>                      | 14.3 | 146.0 |
| 23. <i>Glassia</i>                    | 14.3 | 119.3 |
| 24. <i>Skenidioides</i>               | 14.3 | 116.7 |
| 25. <i>Strophochonetes</i>            | 14.3 | 68.2  |
| 26. <i>Gypidula</i>                   | 14.3 | 54.4  |
| 27. <i>Meristina</i>                  | 14.3 | 19.6  |
| 28. <i>Concludium</i>                 | 7.1  | 221.6 |
| 29. <i>Protochonetes ludloviensis</i> | 7.1  | 57.8  |
| 30. <i>Lissatrypa</i>                 | 7.1  | 17.4  |
| 31. <i>Dicoelosia biloba</i>          | 7.1  | 12.3  |
| 32. <i>Eospirifer</i>                 | 7.1  | 12.3  |
| 33. Athyrids                          | 7.1  | 9.3   |
| 34. <i>Schizotreta</i>                | 7.1  | 3.4   |

Number of collections studied = 14  
Species density = 10.4

Homogeneity = 55.61%  
Distinctness coefficient = 40.0%

of a continuous gradient from the *Salopina* community increasing through the *Homoeospira/Sphaerirhynchia* and *Isorthis* communities, and reaching the highest values in the *Dicoelosia* community.

In the Ludlow, the *Isorthis* community is more highly dominated by *Isorthis* spp. than in the Wenlock. In the earlier part of the Wenlock the fauna is usually dominated by *Eospirifer radiatus* or *Striispirifer plicatellus*, while *Isorthis* is often rare. The Ludlow *Isorthis* community still maintains its ecological position between the *Sphaerirhynchia* and *Dicoelosia* communities, and so it occupies the same range of environment as in the Wenlock, despite the increase in *Isorthis* itself.

#### 4. *Dicoelosia* community (Tables 8 and 9)

Bivalves are uncommon in the *Dicoelosia* community, but trilobites are frequently found, and orthocone nautiloids and graptolites, while not members of the living benthonic community, are sometimes present in the thanatocoenose.

TABLE 8. Composition of the Wenlock *Dicoelosia* community.

#### WENLOCK

##### DICOELOSIA COMMUNITY

| PREVALENT SPECIES                        | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|--|---------------------|--------------------|
| 1. <i>Leangella</i>                      | 100·0               | 764·6              |
| 2. <i>Dicoelosia biloba</i>              | 77·8                | 1765·3             |
| 3. <i>Eospirifer</i>                     | 77·8                | 451·3              |
| 4. <i>Skenidioides</i>                   | 77·8                | 372·8              |
| 5. <i>Dalejina</i>                       | 77·8                | 283·2              |
| 6. <i>Eoplectodonta</i> spp.             | 77·8                | 262·6              |
| 7. <i>Atrypa</i>                         | 66·7                | 253·0              |
| 8. <i>Resserella canalis</i>             | 66·7                | 216·8              |
| 9. <i>Atrypina</i>                       | 66·7                | 152·8              |
| 10. <i>Howellella</i> spp.               | 55·6                | 328·4              |
| 11. <i>Isorthis</i>                      | 55·6                | 262·1              |
| 12. <i>Craniops</i>                      | 55·6                | 248·6              |
| 13. Orthids                              | 55·6                | 63·2               |
| 14. <i>Resserella sabrinae</i>           | 44·4                | 451·8              |
| 15. <i>Mesopholidostrophia</i> spp.      | 44·4                | 209·9              |
| 16. <i>Glassia</i>                       | 44·4                | 63·3               |
| 17. <i>Streptis</i>                      | 44·4                | 40·8               |
| OTHER SPECIES                            |                     |                    |
| 18. <i>Protochonetes minimus</i>         | 33·3                | 945·0              |
| 19. <i>Lissatrypa</i>                    | 33·3                | 322·2              |
| 20. <i>Nucleospira</i>                   | 33·3                | 37·7               |
| 21. <i>Leptaena</i> aff. <i>purpurea</i> | 33·3                | 37·3               |
| 22. <i>Lingula</i>                       | 33·3                | 33·7               |
| 23. <i>Leptostrophia filosa</i>          | 33·3                | 29·1               |
| 24. <i>Cordatomyonia edgelliana</i>      | 22·2                | 318·4              |
| 25. <i>Anastrophia</i>                   | 22·2                | 135·8              |
| 26. cf. <i>Visbyella trewerna</i>        | 22·2                | 105·8              |
| 27. <i>Shagamella</i>                    | 22·2                | 91·7               |
| 28. <i>Striispirifer</i>                 | 22·2                | 67·4               |
| 29. <i>Whitfieldella</i>                 | 22·2                | 52·2               |
| 30. <i>Cyrtia</i>                        | 22·2                | 36·4               |

TABLE 8 (cont.):

| OTHER SPECIES                              | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|--|---------------------|--------------------|
| 31. <i>Hyattidina</i>                      | 22.2                | 20.7               |
| 32. <i>Dolerorthis</i> spp.                | 22.2                | 20.4               |
| 33. <i>Gypidula</i>                        | 22.2                | 19.6               |
| 34. <i>Salopina</i>                        | 22.2                | 11.1               |
| 35. <i>Trigonirhynchia</i>                 | 11.1                | 61.8               |
| 36. <i>Amphistrophia</i> spp.              | 11.1                | 58.9               |
| 37. <i>Orbiculoidea</i>                    | 11.1                | 50.9               |
| 38. <i>Coolinia</i>                        | 11.1                | 37.8               |
| 39. <i>Protochonetes</i> sp.               | 11.1                | 30.9               |
| 40. <i>Mesoumia</i>                        | 11.1                | 28.7               |
| 41. <i>Sphaerirhynchia wilsoni</i>         | 11.1                | 25.4               |
| 42. <i>Dictyonella</i>                     | 11.1                | 20.4               |
| 43. <i>Meristina</i>                       | 11.1                | 16.7               |
| 44. <i>Clorinda</i> sp.                    | 11.1                | 11.1               |
| 45. ? <i>Eridorthis</i>                    | 11.1                | 11.1               |
| 46. <i>Plectatrypa</i>                     | 11.1                | 9.6                |
| 47. ' <i>Camarotoechia</i> ' <i>nucula</i> | 11.1                | 5.6                |

Number of collections studied = 9  
Species density = 16.8

Homogeneity = 64.31%  
Distinctness coefficient = 52.9%

TABLE 9. Composition of the Ludlow *Dicoelosia* community.

## LUDLOW

## DICOELOSIA COMMUNITY

| PREVALENT SPECIES                        | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|--|---------------------|--------------------|
| 1. <i>Isorthis</i>                       | 88.9                | 1171.1             |
| 2. <i>Dalejina</i>                       | 88.9                | 872.7              |
| 3. <i>Howellella</i> spp.                | 88.9                | 645.8              |
| 4. <i>Protochonetes minimus</i>          | 88.9                | 604.3              |
| 5. <i>Skenidioides</i>                   | 88.9                | 521.5              |
| 6. <i>Atrypa</i>                         | 88.9                | 484.1              |
| 7. <i>Dicoelosia biloba</i>              | 77.8                | 745.9              |
| 8. <i>Leptostrophia filosa</i>           | 77.8                | 242.9              |
| 9. <i>Mesopholidostrophia</i> spp.       | 55.6                | 476.9              |
| 10. <i>Shagamella</i>                    | 55.6                | 455.0              |
| 11. <i>Nucleospira</i>                   | 55.6                | 370.7              |
| 12. <i>Aegiria grayi</i>                 | 55.6                | 251.1              |
| 13. <i>Amphistrophia</i> spp.            | 44.4                | 272.6              |
| 14. <i>Craniops</i>                      | 44.4                | 185.0              |
| 15. <i>Cyrtia</i>                        | 44.4                | 129.7              |
| 16. <i>Lingula</i>                       | 44.4                | 100.4              |
| OTHER SPECIES                            |                     |                    |
| 17. <i>Glassia</i>                       | 44.4                | 97.9               |
| 18. <i>Leptaena</i> aff. <i>purpurea</i> | 33.3                | 175.8              |
| 19. <i>Leangella</i>                     | 33.3                | 166.7              |
| 20. <i>Gypidula</i>                      | 33.3                | 106.2              |
| 21. <i>Eospirifer</i>                    | 33.3                | 59.7               |
| 22. <i>Strophonella</i>                  | 22.2                | 68.5               |
| 23. <i>Resserella canalis</i>            | 22.2                | 67.3               |

TABLE 9 (cont.):

| OTHER SPECIES                               | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
|---|---------------------|--------------------|
| 24. <i>Hyattidina</i>                       | 22.2                | 62.1               |
| 25. <i>Whitfieldella</i>                    | 22.2                | 58.2               |
| 26. ' <i>Camarotoecchia</i> ' <i>nucula</i> | 22.2                | 55.2               |
| 27. <i>Sphaerirhynchia wilsoni</i>          | 22.2                | 38.4               |
| 28. Orthids                                 | 22.2                | 37.2               |
| 29. <i>Salopina</i>                         | 22.2                | 29.6               |
| 30. <i>Trigonirhynchia</i>                  | 22.2                | 16.2               |
| 31. <i>Nanospira</i>                        | 11.1                | 56.2               |
| 32. <i>Leptaena</i> spp.                    | 11.1                | 41.1               |
| 33. cf. <i>Visbyella trewerna</i>           | 11.1                | 40.6               |
| 34. <i>Rhynchotreta cuneata</i>             | 11.1                | 25.8               |
| 35. Athyrids                                | 11.1                | 25.6               |
| 36. <i>Katastrophiomena</i>                 | 11.1                | 21.8               |
| 37. <i>Coolinia</i>                         | 11.1                | 8.6                |
| 38. <i>Striispirifer</i>                    | 11.1                | 7.8                |

Number of collections studied = 9      Homogeneity = 69.30%  
Species density = 15.6                      Distinctness coefficient = 43.7%

The community is characterized by brachiopod species with a small adult size, such as *Skenidioides lewisii*, *Dicoelosia biloba*, *Streptis grayii*, *Protochonetes minimus*, and plectambonitid species. Another characteristic feature is the lack of dominant species in contrast to the *Salopina* community.

The Wenlock and Ludlow *Dicoelosia* communities differ slightly in species composition. *Isorthis* is much more common in the Ludlow than the Wenlock, while *Leangella segmentum*, *Eoplectodonta duvalii*, and *Streptis* are important in the Wenlock, but rare in the Ludlow; indeed *Eoplectodonta* and *Streptis* have not been recorded in the bulk collections, and are therefore absent from Table 9.

#### 5. *Visbyella* community (Table 10 for Wenlock only)

Certain species are virtually restricted to the *Visbyella* community (Hancock, Hurst and Fürsich 1974). In this class are *Visbyella trewerna* and another tiny resserellid very similar to *Visbyella* (Bassett 1970-1972), '*Clorinda*' *dormitzeri*, *Bracteoleptaena*, *Mesounia*, and the bivalve *Cardiola interrupta*. Ostracods are often abundant, and pelagic groups, notably orthocones and graptolites, are commonly preserved with the benthonic assemblage.

TABLE 10. Composition of the Wenlock *Visbyella* community.

| WENLOCK                                  |                     |                    |
|--|---------------------|--------------------|
| <i>VISBYELLA</i> COMMUNITY               |                     |                    |
| PREVALENT SPECIES                        | PRESENCE PERCENTAGE | FREQUENCY PRESENCE |
| 1. cf. <i>Visbyella trewerna</i>         | 100.0               | 2268.6             |
| 2. <i>Protochonetes minimus</i>          | 100.0               | 615.8              |
| 3. <i>Glassia</i>                        | 80.0                | 367.2              |
| 4. <i>Leangella</i>                      | 60.0                | 780.2              |
| 5. <i>Lingula</i>                        | 40.0                | 285.6              |
| 6. <i>Hyattidina</i>                     | 40.0                | 184.4              |
| 7. ' <i>Clorinda</i> ' <i>dormitzeri</i> | 40.0                | 49.8               |

TABLE 10 (cont.):

| OTHER SPECIES                            | PRESENCE PERCENTAGE | FREQUENCY PRESENCE               |
|--|---------------------|----------------------------------|
| 8. <i>Bracteoleptaena</i>                | 20.0                | 142.8                            |
| 9. <i>Strophochonetes</i>                | 20.0                | 107.0                            |
| 10. <i>Aegiria grayi</i>                 | 20.0                | 83.2                             |
| 11. <i>Cyrtia</i>                        | 20.0                | 53.4                             |
| 12. <i>Nucleospira</i>                   | 20.0                | 35.6                             |
| 13. <i>Mesounia</i>                      | 20.0                | 35.6                             |
| 14. <i>Craniops</i>                      | 20.0                | 35.6                             |
| 15. Orthids                              | 20.0                | 32.0                             |
| 16. <i>Eospirifer</i>                    | 20.0                | 32.0                             |
| 17. <i>Dalejina</i>                      | 20.0                | 25.0                             |
| 18. <i>Isorthis</i>                      | 20.0                | 25.0                             |
| 19. <i>Leptaena</i> aff. <i>purpurea</i> | 20.0                | 17.8                             |
| Number of collections studied = 5        |                     | Homogeneity = 63.89%             |
| Species density = 7.2                    |                     | Distinctness coefficient = 85.7% |

Coming beyond the *Dicoelosia* community, where the highest species density (diversity) values are found, the *Visbyella* community contrasts strongly in having a species density as low as that of the *Salopina* community. Individual collections generally contain one to three rare species, and only collection DB-C-1 is anomalous, with seven.

#### *Distribution of individual species*

The ecological distribution of each species in the complete brachiopod fauna is summarized in Table 11 (see also text-fig. 3). The fidelity columns show that most species occur in two or more communities. However, even the most tolerant species (those occurring in four or five communities) are usually very rare in one of their communities of occurrence and can be looked on as occurring there accidentally.

TABLE 11. Ecological distribution of individual species.

| SPECIES                       | WENLOCK                  |          | LUDLOW                   |          |
|-------------------------------|--------------------------|----------|--------------------------|----------|
|                               | COMMUNITY IN WHICH MODAL | FIDELITY | COMMUNITY IN WHICH MODAL | FIDELITY |
| <i>Lingula</i>                | <i>Visbyella</i>         | 4        | <i>Sphaerirhynchia</i>   | 4        |
| <i>Craniops</i>               | <i>Isorthis</i>          | 5        | <i>Dicoelosia</i>        | 4        |
| <i>Dinobolus</i>              | <i>Isorthis</i>          | 1        |                          |          |
| <i>Schizocrania</i>           |                          |          | <i>Salopina</i>          | 1        |
| <i>Orbiculoidea</i>           | <i>Dicoelosia</i>        | 3        | <i>Salopina</i>          | 2        |
| <i>Schizotreta</i>            | <i>Salopina</i>          | 1        | <i>Salopina</i>          | 2        |
| <i>Dolerorthis</i> spp.       | <i>Dicoelosia</i>        | 1        |                          |          |
| ? <i>Eridorthis</i>           | <i>Dicoelosia</i>        | 1        |                          |          |
| Orthids                       | <i>Dicoelosia</i>        | 3        | <i>Dicoelosia</i>        | 1        |
| <i>Skenidioides</i>           | <i>Dicoelosia</i>        | 2        | <i>Dicoelosia</i>        | 2        |
| <i>Salopina</i> spp.          | <i>Salopina</i>          | 4        | <i>Salopina</i>          | 4        |
| <i>Isorthis</i> spp.          | <i>Isorthis</i>          | 4        | <i>Isorthis</i>          | 4        |
| <i>Resserella canalis</i>     | <i>Isorthis</i>          | 3        | <i>Dicoelosia</i>        | 1        |
| <i>Resserella sabrinae</i>    | <i>Dicoelosia</i>        | 1        |                          |          |
| cf. <i>Visbyella trewerna</i> | <i>Visbyella</i>         | 2        | <i>Visbyella</i>         | 2        |
| <i>Dicoelosia biloba</i>      | <i>Dicoelosia</i>        | 1        | <i>Dicoelosia</i>        | 2        |
| <i>Dalejina</i>               | <i>Dicoelosia</i>        | 4        | <i>Isorthis</i>          | 2        |



TABLE 11 (cont.):

| SPECIES                                       | WENLOCK                  |          | LUDLOW                   |          |
|---|--------------------------|----------|--------------------------|----------|
|   | COMMUNITY IN WHICH MODAL | FIDELITY | COMMUNITY IN WHICH MODAL | FIDELITY |
| <i>Marklandella</i>                           | <i>Salopina</i>          | 2        |                          |          |
| <i>Cordatomyonia edgelliana</i>               | <i>Dicoelosia</i>        | 3        |                          |          |
| <i>Streptis</i>                               | <i>Dicoelosia</i>        | 1        |                          |          |
| <i>Dictyonella</i>                            | <i>Dicoelosia</i>        | 2        |                          |          |
| <i>Mesounia</i>                               | <i>Visbyella</i>         | 2        |                          |          |
| <i>Leangella</i>                              | <i>Visbyella</i>         | 3        | <i>Dicoelosia</i>        | 1        |
| <i>Eoplectodonta</i> spp.                     | <i>Isorthis</i>          | 2        |                          |          |
| <i>Aegiria grayi</i>                          | <i>Visbyella</i>         | 2        | <i>Visbyella</i>         | 3        |
| <i>Katastrophomena</i>                        | <i>Isorthis</i>          | 1        | <i>Dicoelosia</i>        | 1        |
| <i>Leptaena</i> spp.                          | <i>Isorthis</i>          | 3        | <i>Isorthis</i>          | 4        |
| <i>Leptaena</i> aff. <i>purpurea</i>          | <i>Dicoelosia</i>        | 3        | <i>Dicoelosia</i>        | 1        |
| <i>Bracteoleptaena</i>                        | <i>Visbyella</i>         | 1        |                          |          |
| <i>Leptostrophia compressa</i>                | <i>Isorthis</i>          | 1        |                          |          |
| <i>Leptostrophia filosa</i>                   | <i>Homoeospira</i>       | 4        | <i>Sphaerirhynchia</i>   | 4        |
| <i>Brachyprion</i>                            | <i>Homoeospira</i>       | 2        |                          |          |
| <i>Protomegastrophia</i>                      | <i>Homoeospira</i>       | 2        |                          |          |
| <i>Mclearnites</i>                            | <i>Salopina</i>          | 2        |                          |          |
| <i>Amphistrophia</i> spp.                     | <i>Isorthis</i>          | 4        | <i>Dicoelosia</i>        | 3        |
| <i>A.</i> ( <i>Pembrostrophia</i> )           | <i>Salopina</i>          | 2        |                          |          |
| <i>Mesopholidostrophia</i> spp.               | <i>Dicoelosia</i>        | 2        | <i>Isorthis</i>          | 3        |
| <i>Strophonella</i>                           | <i>Isorthis</i>          | 2        | <i>Isorthis</i>          | 3        |
| <i>Shaleria</i>                               |                          |          | <i>Isorthis</i>          | 2        |
| <i>Coolinia</i>                               | <i>Isorthis</i>          | 4        | <i>Isorthis</i>          | 2        |
| <i>Strophochonetes</i>                        | <i>Salopina</i>          | 4        | <i>Isorthis</i>          | 3        |
| <i>Protochonetes</i> spp.                     | <i>Salopina</i>          | 4        | <i>Salopina</i>          | 3        |
| <i>Protochonetes minimus</i>                  | <i>Dicoelosia</i>        | 4        | <i>Dicoelosia</i>        | 4        |
| <i>Shagamella</i>                             | <i>Dicoelosia</i>        | 3        | <i>Isorthis</i>          | 3        |
| <i>Anastrophia</i>                            | <i>Isorthis</i>          | 2        |                          |          |
| <i>Conchidium</i>                             |                          |          | <i>Isorthis</i>          | 1        |
| <i>Gypidula</i>                               | <i>Homoeospira</i>       | 4        | <i>Dicoelosia</i>        | 3        |
| <i>Clorinda</i> sp.                           | <i>Isorthis</i>          | 2        |                          |          |
| ' <i>Clorinda</i> ' <i>dormitzeri</i>         | <i>Visbyella</i>         | 1        | <i>Visbyella</i>         | 1        |
| ' <i>Camarotoechia</i> ' <i>llandoveriana</i> | <i>Salopina</i>          | 1        |                          |          |
| ' <i>Camarotoechia</i> ' <i>nucula</i>        | <i>Salopina</i>          | 4        | <i>Salopina</i>          | 4        |
| ' <i>Camarotoechia</i> ' <i>tripartita</i>    | <i>Salopina</i>          | 1        | <i>Salopina</i>          | 1        |
| <i>Trigonirhynchia</i>                        | <i>Isorthis</i>          | 2        | <i>Sphaerirhynchia</i>   | 2        |
| <i>Rhynchotreta cuneata</i>                   | <i>Salopina</i>          | 2        | <i>Dicoelosia</i>        | 1        |
| <i>Sphaerirhynchia wilsoni</i>                | <i>Homoeospira</i>       | 4        | <i>Sphaerirhynchia</i>   | 4        |
| <i>Sphaerirhynchia davidsoni</i>              | <i>Salopina</i>          | 2        |                          |          |
| Rhynchonellids                                | <i>Salopina</i>          | 1        |                          |          |
| <i>Atrypina</i>                               | <i>Dicoelosia</i>        | 2        |                          |          |
| <i>Plectatrypa</i>                            | <i>Dicoelosia</i>        | 1        |                          |          |
| <i>Spirigerina</i>                            | <i>Isorthis</i>          | 1        |                          |          |
| <i>Atrypa</i>                                 | <i>Homoeospira</i>       | 4        | <i>Isorthis</i>          | 4        |
| <i>Lissatrypa</i>                             | <i>Dicoelosia</i>        | 1        | <i>Isorthis</i>          | 1        |
| <i>Glassia</i>                                | <i>Visbyella</i>         | 2        | <i>Isorthis</i>          | 3        |
| <i>Nanospira</i>                              |                          |          | <i>Dicoelosia</i>        | 1        |
| <i>Dayia</i>                                  |                          |          | <i>Sphaerirhynchia</i>   | 3        |
| <i>Eocoelia angelini</i>                      | <i>Salopina</i>          | 3        |                          |          |
| <i>Homoeospira</i>                            | <i>Homoeospira</i>       | 3        | <i>Isorthis</i>          | 2        |

TABLE 11 (cont.):

| SPECIES                | WENLOCK                  |          | LUDLOW                   |          |
|------------------------|--------------------------|----------|--------------------------|----------|
|                        | COMMUNITY IN WHICH MODAL | FIDELITY | COMMUNITY IN WHICH MODAL | FIDELITY |
| <i>Meristina</i>       | <i>Isorthis</i>          | 4        | <i>Isorthis</i>          | 1        |
| <i>Hyattidina</i>      | <i>Visbyella</i>         | 4        | <i>Visbyella</i>         | 3        |
| <i>Whitfieldella</i>   | <i>Isorthis</i>          | 4        | <i>Sphaerirhynchia</i>   | 4        |
| <i>Nucleospira</i>     | <i>Dicoelosia</i>        | 4        | <i>Dicoelosia</i>        | 2        |
| Athyrids               | <i>Isorthis</i>          | 3        | <i>Dicoelosia</i>        | 2        |
| <i>Cyrtia</i>          | <i>Visbyella</i>         | 3        | <i>Dicoelosia</i>        | 1        |
| <i>Eospirifer</i>      | <i>Dicoelosia</i>        | 5        | <i>Dicoelosia</i>        | 2        |
| <i>Striispirifer</i>   | <i>Isorthis</i>          | 4        | <i>Dicoelosia</i>        | 1        |
| <i>Howellella</i> spp. | <i>Homoeospira</i>       | 4        | <i>Sphaerirhynchia</i>   | 4        |

## EXPLANATION OF PLATE 106

All specimens are decalcified internal moulds, treated with ammonium chloride. Grid references are in the Appendix, or given below.

Figs. 1, 2. *Salopina lunata* (J. de C. Sowerby). Wood Green Railway Cutting, May Hill (Grid ref. SO 6943.1664). 1, pedicle valve,  $\times 2$ . 2, brachial valve,  $\times 2$ .

Fig. 3. *Protochonetes ludloviensis* Muir-Wood. Pedicle valve,  $\times 2$ , locality as Fig. 1.

Fig. 4. '*Camarotoechia*' *nucula* (J. de C. Sowerby). Brachial valve,  $\times 2\frac{1}{2}$ , locality as Fig. 1.

Figs. 5, 6. *Homoeospira* cf. *H. baylei* (Davidson). Coll. LD-S-4. 5, pedicle valve, BC 33721,  $\times 2\frac{1}{2}$ . 6, brachial valve, BC 33748,  $\times 2\frac{1}{2}$ .

Fig. 7. *Howellella* sp. Brachial valve BC 33852,  $\times 2\frac{1}{2}$ , coll. LD-S-4.

Fig. 8. *Dayianavicula* (J. de C. Sowerby). Pedicle valve,  $\times 2$ , Downton, near Ludlow (Grid ref. SO 4311.7314).

Fig. 9. Bivalves and gastropods in the *Salopina* community,  $\times 1$ , coll. FE-3.

Figs. 10, 11. *Sphaerirhynchia wilsoni* (J. Sowerby). 10, pedicle valve, BC 21268,  $\times 2$ , coll. SG-21. 11, brachial valve,  $\times 2$ , Sawdde Gorge (Grid ref. SN 7250.2482).

Fig. 12. *Leptostrophia filosa* (J. de C. Sowerby). Pedicle valve,  $\times 1\frac{1}{2}$ , Sawdde Gorge (Grid ref. SN 7250.2482).

Fig. 13. *Atrypa reticularis* (Linnaeus). Pedicle valve, BC 31840,  $\times 1$ , coll. LD-S-2.

Figs. 14, 15. *Isorthis orbicularis* (J. de C. Sowerby). 14, pedicle valve, BC 25776,  $\times 2$ , coll. Usk 4. 15, brachial valve, BC 25209,  $\times 2$ , coll. Usk 5.

Fig. 16. *Mesopholidostrophia* sp. Pedicle valve,  $\times 2$ , Elton Beds, Ludlow.

Fig. 17. *Eospirifer radiatus* (J. de C. Sowerby). Pedicle valve, BC 30618,  $\times 1\frac{1}{2}$ , coll. LD-S-16.

Fig. 18. *Dalejina hybrida* (J. de C. Sowerby). Pedicle valve, BC 20684,  $\times 1\frac{1}{2}$ , coll. SG-16.

Fig. 19. *Dicoelosia biloba* (Linnaeus). Pedicle valve,  $\times 3$ , Elton Beds, Ludlow.

Fig. 20. *Streptis grayii* (Davidson). Pedicle valve,  $\times 2$ , Kilbride Peninsula, Co. Mayo, Ireland.

Fig. 21. *Eoplectodonta duvalii* (Davidson). Brachial valve, BC 30416,  $\times 1\frac{1}{2}$ , coll. LD-S-11.

Fig. 22. *Gypidula galeata* (Dalman). Pedicle valve, BC 28106,  $\times 2$ , coll. Lud 10.

Fig. 23. *Amphistrophia fuciculata* (M'Coy). Pedicle valve, BC 30995,  $\times 2$ , coll. LD-S-17.

Fig. 24. *Lingula* sp. BC 42065,  $\times 2$ , coll. 69-A.

Fig. 25. *Dolerorthis* sp. Brachial valve,  $\times 1\frac{1}{2}$ , Kilbride Peninsula, Co. Mayo, Ireland.

Fig. 26. *Skenidioides lewisii* (Davidson). Brachial valve,  $\times 3$ , Elton Beds, Ludlow.

Fig. 27. *Leangella segmentum* (Lindström). Pedicle valve, BC 30263,  $\times 2\frac{1}{2}$ , coll. LD-S-14.

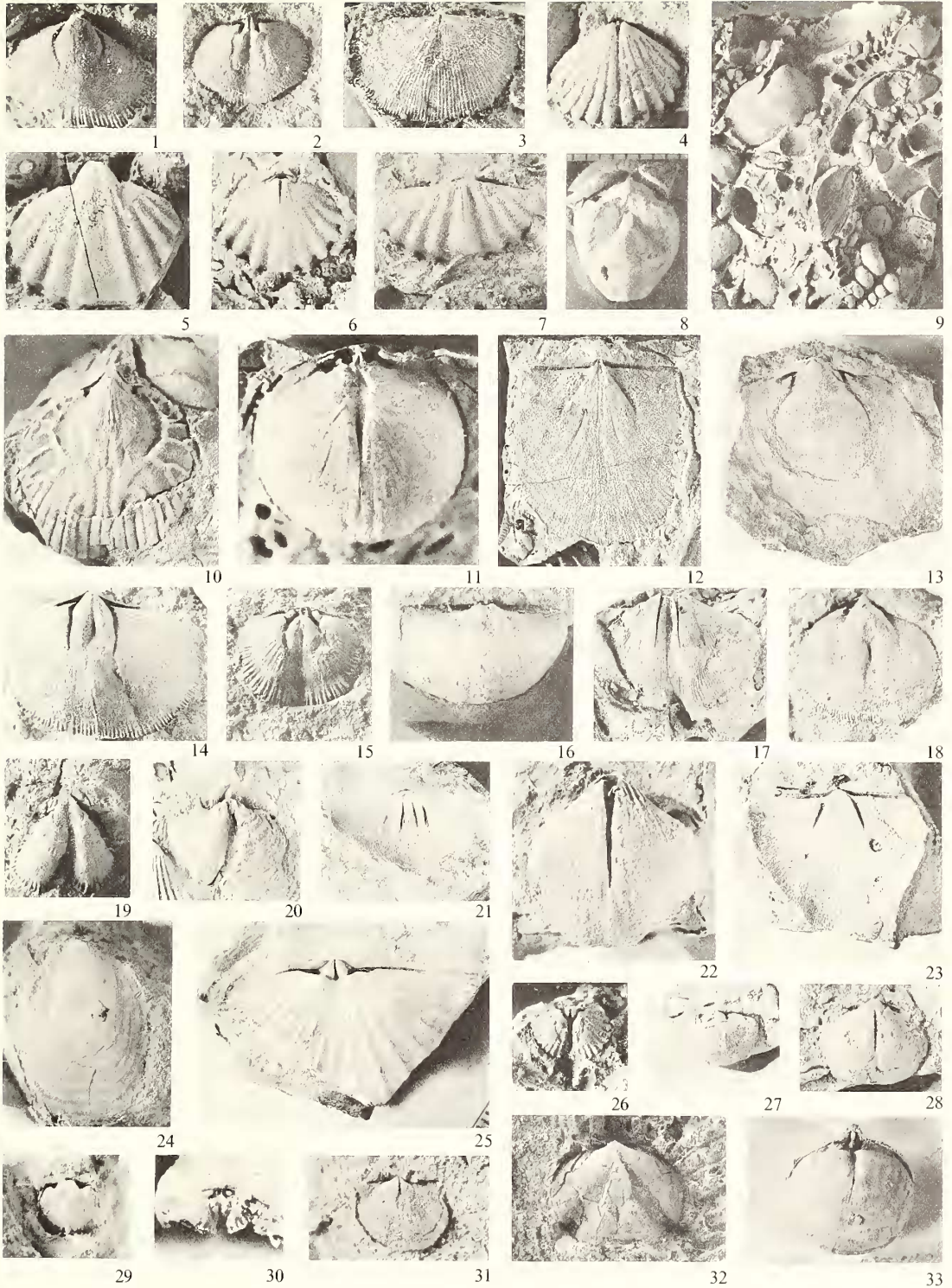
Fig. 28. *Nucleospira pisum* (J. de C. Sowerby). Pedicle valve,  $\times 2\frac{1}{2}$ , coll. W-N-2.

Figs. 29, 30. Cf. *Visbyella trewerna* Bassett. 29, pedicle valve, BC 36015,  $\times 3$ , coll. PS-N-1. 30, brachial valve,  $\times 3$ , coll. B.L.II.

Fig. 31. *Protochonetes minimus* (J. de C. Sowerby). Pedicle valve, BC 24649,  $\times 4$ , coll. Usk 2.

Fig. 32. '*Clorinda*' *dormitzeri* (Barrande). Brachial valve, GSM DT6061,  $\times 3$ , North Wales. Negative supplied by Dr. M. G. Bassett.

Fig. 33. *Glassia* sp. Brachial valve, BC 30450,  $\times 2\frac{1}{2}$ , coll. LD-S-11.





Those species which are confined to one community are usually exceedingly rare, being represented in the total collections by only a few specimens. For example, there are only two specimens of *Schizocrania* out of a total fauna of more than 20,000 specimens.

#### *Other associations*

A few collections do not easily fit into any of the main communities. They all have a high dominance of one or two species, ones which are otherwise usually quite rare. They may be highly distinctive assemblages living in atypical and rare environments; alternatively they could represent clusters of rare species, or population explosions of opportunistic species (Levinton 1970).

A single collection from the basal Downtonian of May Hill contains 98% *Lingula* (MH-11, see Appendix), and faunas with a abundant *Lingula* occur in the *Platyschisma* Beds low in the Downtonian at Knighton (Holland 1959) and Ludlow (Holland 1962). These rare assemblages resemble the Llandovery *Lingula* community (Ziegler *et al.* 1968) and particularly the 'restricted' *Lingula* community (Ziegler *et al.* 1969) which contains *Lingula* alone.

Assemblages dominated by bivalves have been obtained at several localities in the Wenlock (see Appendix) and about a metre above the Ludlow Bone Bed at Ludlow. Characteristic genera for this association are *Actinodonta*, *Nuculites*, large pteroids, and modiomorphaceans. *Nucula* and *Grammysia* also occur. Brachiopods characteristic of the *Salopina* community may be present, particularly '*Camarotoechia*' *nucula*, *Salopina*, and *Lingula*. In contrast to the main communities described above, the Bivalve association is predominantly infaunal, with free-burrowing species and endobysate forms (Stanley 1972). It, too, resembles some developments of the Llandovery *Lingula* community.

Three Wenlock collections have been grouped as the *Resserella* association which is dominated by *R. whitfieldensis* (Bassett 1972, p. 50). The other species in the collections suggest that this association is most closely related to the *Homoeospira* community.

In the Ludlow a *Dayia*-dominated association shares most of its genera with the *Sphaerirhynchia* community. Virtually monospecific assemblages of *Dayia navicula* occur through large sedimentary thicknesses at Builth Wells, which suggests either that this species could colonize areas of the sea-floor inimical to other brachiopods of the *Sphaerirhynchia* community, or that its presence in dense concentrations excluded other species populations. Thus the *Dayia* association is identified by having a limited number of species rather than by species peculiar to the association.

The *Gypidula*/*Atrypa* association is dominated equally by *Gypidula galeata* and *Atrypa reticularis*. The assemblage is found more frequently in limestones than clastic sediments. The group of species associated with *Gypidula* and *Atrypa* varies, so in different cases the assemblage most closely resembles *Isorthis*, *Homoeospira*/*Sphaerirhynchia*, or *Salopina* communities.

#### *Relations between communities*

The individualistic hypothesis of the community proposed by Gleason (1926) holds that communities are combinations of organisms which, in responding to

similar ecological requirements, happen to occur together. The theory stresses the individual response of the organisms to the environment. Their interaction is of secondary importance. The applicability of this idea to the Silurian is indicated by the variability (low homogeneity) of the communities and also by their continuously intergrading nature.

The primary influence of the environment in determining the structure of an association leads to a corollary of the individualistic hypothesis: the concept of the continuum. Along an environmental gradient species composition changes until, by degrees, one community is replaced by another. The rate of compositional change is proportional to the steepness of the gradient. The compositional and geographical boundaries dividing communities are arbitrary since no natural hiatus exists. The continuum is demonstrated in text-fig. 3 where a selection of species is plotted to show their frequency presence values through the full community spectrum or environmental gradient for both the Wenlock and the Ludlow. With one exception, all the curves are unimodal and show the gradual changes from one community to the next. Another striking feature of text-fig. 3 is the similarity of the Wenlock and Ludlow curves for many species.

The continuum is also expressed by the similarity coefficient (see Table 1) between communities. Text-fig. 4 shows the value of the similarity coefficient between each community and the *Salopina* community in the Wenlock and the Ludlow. The progressive fall in value towards the *Visbyella* community reflects the decreasing number of species in common, and the diverging values of frequency presence of those species which remain.

#### ENVIRONMENTAL INTERPRETATION

Studies on Recent communities (Thorson 1957) have repeatedly shown a relation between depth of water and community. Studies in Lower Palaeozoic fossil communities point to the same conclusion (Ziegler 1965; Bayer 1967; Seilacher 1967; Bretsky 1969). In this section we present evidence indicating that Wenlock and Ludlow communities occupied progressively deeper marine environments from the *Salopina* community the shallowest, through *Homoeospira/Sphaerirhynchia* and *Isorthis*, to the deeper *Dicoelosia* community. The ecology of the *Visbyella* community is discussed briefly in a later section.

Apart from the normal correlation of lithology with depth (i.e. little coarse sediment in deep water), no good correlation has been seen between sediment type and community within the clastic facies covered by this paper.

Temperature control has been put forward by Berry and Boucot (1967), but temperatures were regarded by them as normally being depth related. There is no independent evidence to enable the determination of palaeo-temperatures.

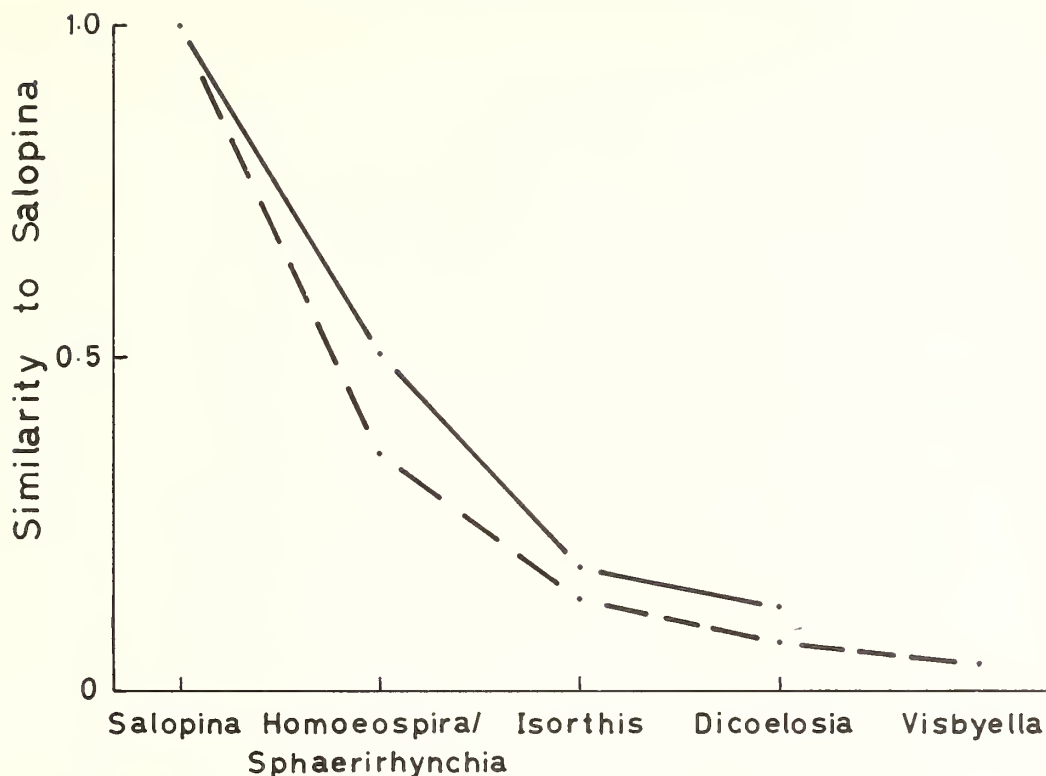
#### *Analogy with previously studied communities*

Ziegler, Cocks and Bambach (1968) defined five depth-related communities in the Llandovery, in order of increasing depth: (1) *Lingula* community, (2) *Eocoelia* community, (3) *Pentamerus* community, (4) *Stricklandia* community, and (5) *Clorinda* community. A still deeper (6) 'Marginal' *Clorinda* community has been described by





TEXT-FIG. 3. Abundance of selected genera in the communities for the Wenlock (dashed lines) and Ludlow (solid lines). Sa—*Salopina* community, Ho/Sp—*Homoeospira/Sphaerirhynchia* community, Is—*Isorthis* community, Di—*Dicoelosia* community, V—*Visbyella* community.



TEXT-FIG. 4. Similarity of each community to the *Salopina* community as calculated with the Similarity Coefficient (Table 1). Dashed line for the Wenlock; solid line for the Ludlow.

Cocks and Rickards (1969). Many genera of brachiopod living during the Llandovery survived into the Wenlock and Ludlow and thus form links between Llandovery and later Silurian communities. Table 12, which lists the modal communities of some of these genera in the upper Llandovery, Wenlock, and Ludlow, shows that the *Dicoelosia* community is the approximate later Silurian equivalent of the *Clorinda* community, *Isorthis* of the *Stricklandia*, *Homoeospira/Sphaerirhynchia* of the *Pentamerus*, and *Salopina* of the *Eocoelia* community. If we assume that similar ecological controls applied in the Wenlock and Ludlow to those in the Llandovery, then it follows that Wenlock and Ludlow communities were also depth related.

#### *Sedimentary and stratigraphic relationships*

At the Sawdde Gorge, the Llandovery exhibits a deepening from the *Eocoelia* community to the *Costistricklandia* community. The Wenlock (text-fig. 5) begins with the *Dicoelosia* community and then shows the following sequence of communities: *Dicoelosia-Isorthis-Homoeospira/Sphaerirhynchia-Salopina*. The *Salopina* community occurs in sediments showing flaser-bedding, herring-bone cross-bedding, and other extremely shallow-water features, and these are interbedded with silts containing the Bivalve association. The Wenlock succession thus records a progressive shallowing. An abrupt change occurs from the topmost Wenlock *Salopina* community

TABLE 12. Modal communities of brachiopod genera in the upper Llandovery, Wenlock, and Ludlow. In the upper Llandovery where two communities are given, the first applies to C<sub>1-3</sub>, the second to C<sub>4-6</sub>. Abbreviations as follows: E—*Eocoelia* community, P—*Pentamerus* community, St—*Stricklandia* community, C—*Clorinda* community, Sa—*Salopina* community, H—*Homoospira* community, Sp—*Sphaerirhynchia* community, I—*Isorthis* community, D—*Dicoelosia* community, V—*Visbyella* community.

| Genus                      | Upper      |         |        |
|----------------------------|------------|---------|--------|
|                            | Llandovery | Wenlock | Ludlow |
| <i>Salopina</i>            | E          | Sa      | Sa     |
| <i>Protochonetes</i>       | E          | Sa      | Sa     |
| ' <i>Camarotoechia</i> '   | E          | Sa      | Sa     |
| <i>Howellella</i>          | E          | H       | Sp     |
| <i>Leptostrophia</i>       | E          | H       | Sp     |
| <i>Atrypa</i>              | P-St       | H       | I      |
| <i>Coolinia</i>            | P-C        | I       | I      |
| <i>Mesopholidostrophia</i> | St         | D       | I      |
| <i>Isorthis</i>            | St         | I       | I      |
| <i>Strophonella</i>        | C          | I       | I      |
| <i>Dicoelosia</i>          | C          | D       | D      |
| <i>Resserella</i>          | C          | D       | D      |
| <i>Skenidiooides</i>       | C          | D       | D      |
| <i>Leangella</i>           | C          | V       | D      |
| <i>Cyrtia</i>              | C          | V       | D      |
| <i>Aegiria</i>             | C          | V       | V      |

to the basal Ludlow *Dicoelosia* community, accompanied by an equally sharp change from shallow-water sediments to deep, quiet-water silts and muds. The Ludlow sequence repeats the communities in the same order as in the Wenlock, suggesting a second regression (text-fig. 5). The *Salopina* community is developed in the highest marine beds prior to the continental Trichrûg Beds, the precursor of the Old Red Sandstone (Potter and Price 1965).

Similar relations can be seen at Usk (text-fig. 5), with two regressive sequences, the lower one culminating in the wave- and current-rippled sandstone directly below the Wenlock Limestone and the upper one continuing through the Ludlow into the Old Red Sandstone. A single collection (U-C-1) immediately above the Wenlock Limestone shows the *Isorthis* community, and records an intermediate stage in the post-Wenlock transgression.

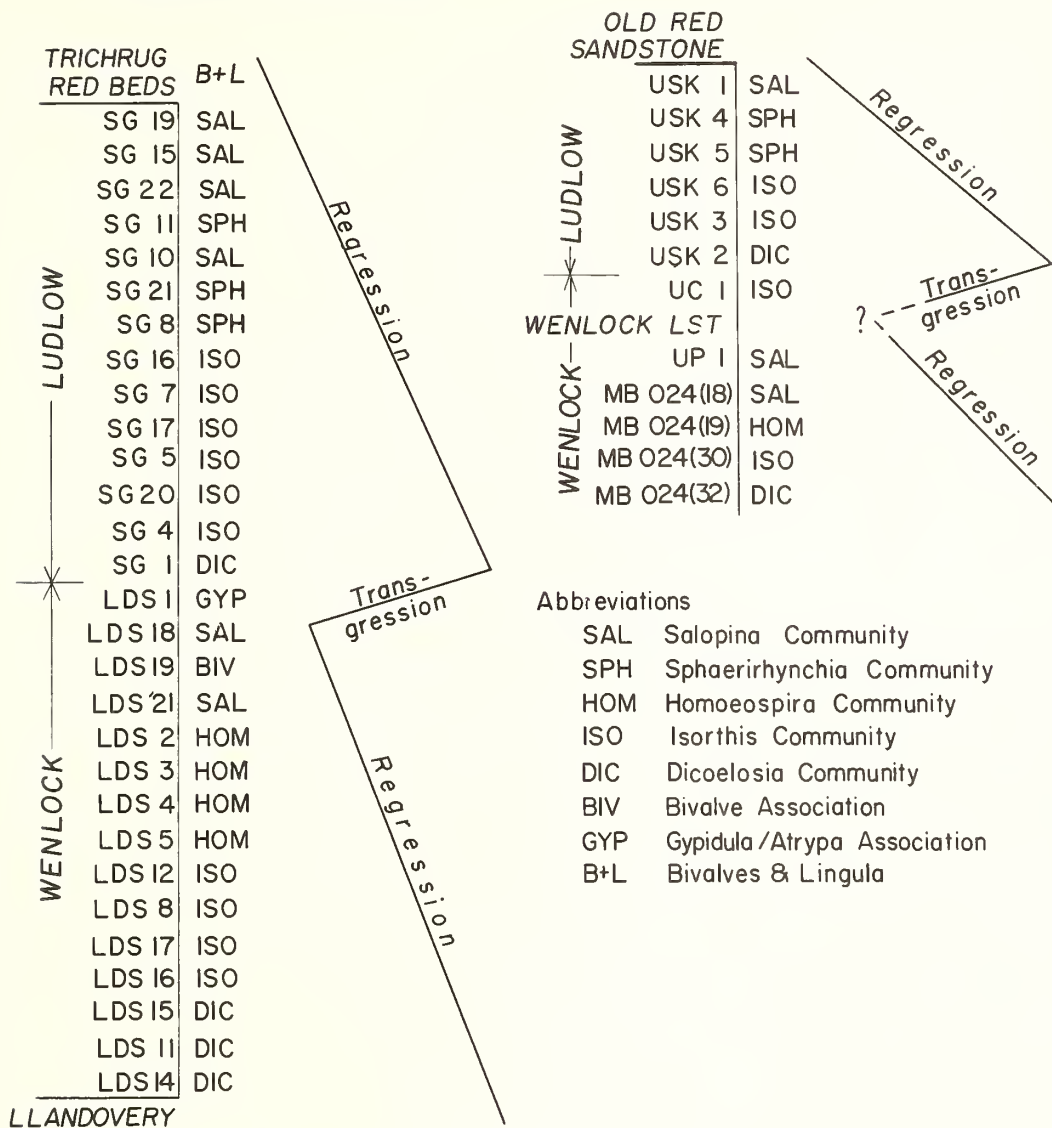
The community succession and the available sedimentary and stratigraphic evidence show the same double regression throughout the Welsh Borderland in each stratigraphic section which has been examined. We have found no evidence of widespread cyclic transgressions and regressions such as those postulated by Phipps and Reeve (1967, fig. 6) for the Malvern Hills area. Shallowing at the end of the Wenlock is further shown by the green algae in the Wenlock Limestone, which are believed by Scoffin (1971) to represent water less than 30 m deep. The Ludlow commences everywhere with the much deeper quiet-water muds of the Eltonian, containing the *Dicoelosia* community.

The sequence of communities during the Ludlow shallowing is modified at Ludlow, where the *Sphaerirhynchia* community is represented by the *Dayia* association.

At the top of the Ludlow and in the basal Downton, the Bivalve association, along with *Lingula*, occurs frequently between the *Salopina* community and the

SAWDDE GORGE

USK



TEXT-FIG. 5. Stratigraphic sequence of collections and their community designations in the Sawdde and Usk sections. The base of the Wenlock Shale is not exposed at Usk, and while there are Ludlow rocks above the Trichrug Beds at Sawdde, no collections were made from them.

fluvial environments of the Old Red Sandstone. Bivalves thus dominated areas shoreward of the *Salopina* community, where sedimentary structures indicate a similar, extremely shallow, depth of water (Allen and Tarlo 1963; Sanzen-Baker 1972).

The double regression cannot be seen in Pembrokeshire, because the Old Red Sandstone appears to have arrived early at Marloes, perhaps even in Wenlock times

(Sanzen-Baker 1972), and the Ludlow shallowing is thus not recorded there. The upper Ludlow in Denbighshire has been removed by erosion, though evidence for a Ludlow shallowing comes from the *Salopina* community preserved in pebbles in the basal Carboniferous (Strahan and Walker 1879).

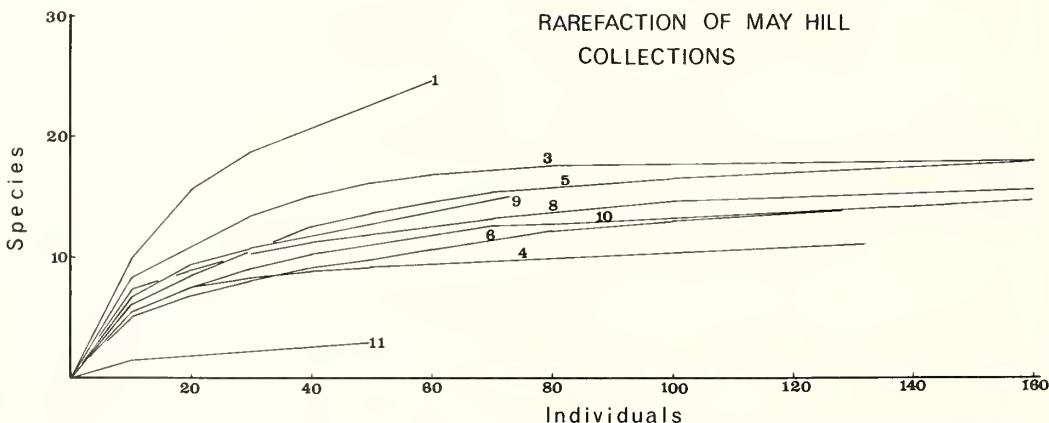
*Possible causes for the depth correlation*

*Stability and predictability.* In modern benthonic communities species diversity increases with depth of water as shown by soft-bottom samples collected along a transect between Gayhead and Bermuda (Sanders and Hessler 1969). The diversity gradient is attributable to the increasing stability and predictability of the environment (Slobodkin and Sanders 1969). A similar gradient is present in our communities.

Sanders's (1968) method for diversity comparisons has been used, treating similar habitats, namely soft, clastic, usually fine-grained, level bottoms of varying depth, and using the brachiopod-bivalve fraction of the collections. The rarefaction technique of Sanders (1968) has been used to avoid the problem of the dependence of the number of species in a collection on the collection size. Rarefaction is used to derive 'expected' values of species diversity at a variety of reduced collection sizes, retaining the relative proportions between species in the original collection. The values form a 'rarefaction curve' (e.g. text-fig. 6). The diversity of different-sized collections is obtained from rarefaction values at a collection size common to each. Text-fig. 6 shows that most curves reach the sixty individual point so this rarefied size has been used for comparisons.

Table 13 lists the diversity values of the collections available at the time of rarefaction computation. The average diversity values for each community form a progression from the low diversity *Salopina* community to the very diverse *Dicoelosia* community. This feature of the depth gradient probably reflects a gradual increase in environmental stability and predictability.

*Food supply.* We have observed a rough gradient in fossil density in our collections. Fossils are very sparse in the deep-water *Dicoelosia* community collections despite the concentrating effect of a continuously slow sedimentation rate in that



TEXT-FIG. 6. Rarefaction curves for May Hill Ludlow collections. Curve numbers refer to MH collections.

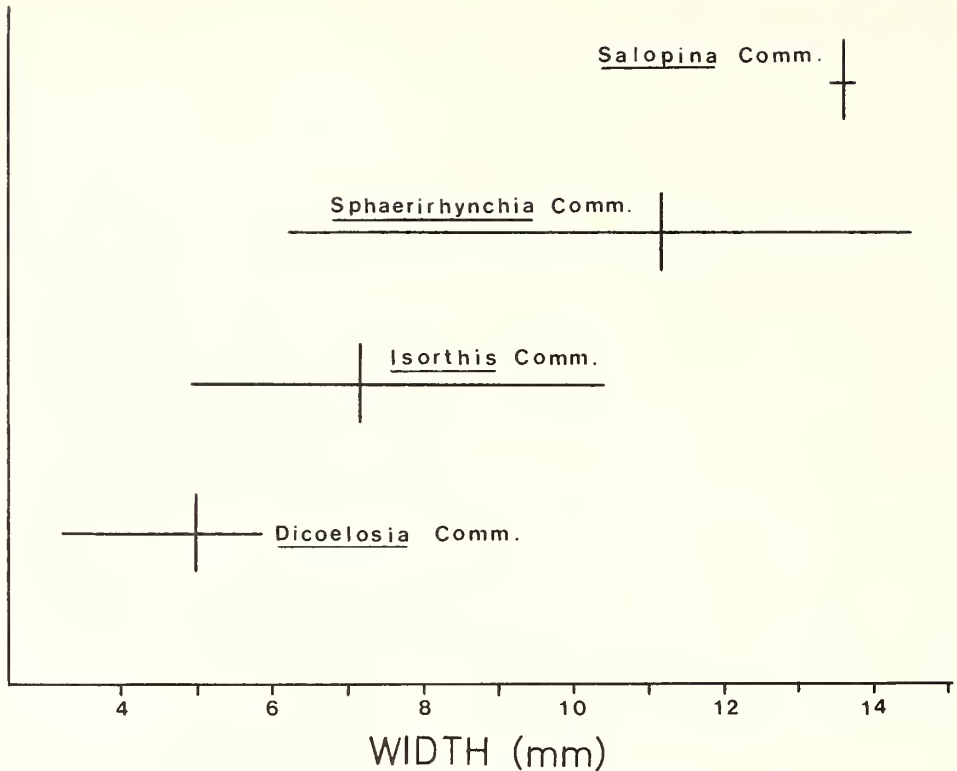


TABLE 13. Diversity of collections grouped into communities, using the 60-individual size derived from the rarefaction method. Values marked \* represent collections of less than 60 individuals and have been obtained by extrapolation.

| <i>Salopina</i><br>community |         | <i>Homoeospira/<br/>Sphaerirhynchia</i><br>community |         | <i>Isorthis</i><br>community |         | <i>Dicoelosia</i><br>community |         |
|------------------------------|---------|--|---------|------------------------------|---------|--------------------------------|---------|
| Lud 5                        | 5.043   | MH-3   | 16.818  | Lud 1                        | 7.513   | 69-A                           | 17.609  |
| Lud 6                        | 7.546   | MH-4   | 9.364   | Lud 2                        | 14.000* | MH-1                           | 24.613  |
| Lud 11                       | 5.579   | MH-8   | 12.511  | Lud 7                        | 11.075  | MH-9                           | 13.753  |
| MH-5                         | 14.636  | Usk 5  | 11.509  | Lud 8                        | 10.502  | Usk 2                          | 11.667  |
| MH-6                         | 11.889  | Usk 4  | 13.358  | EH-1                         | 6.278   | LD-S-15                        | 15.352  |
| MH-10                        | 10.615  | LD-S-4   | 7.326   | EH-2                         | 17.330  | LD-S-13                        | 13.651  |
| BW-4                         | 8.380   | LD-S-3   | 11.304  | Usk 3                        | 16.308  | LD-S-14                        | 13.000* |
| Usk 1                        | 15.263  | LD-S-5   | 20.497  | LD-S-16                      | 20.633  |                                |         |
| LD-S-21                      | 12.579  | LD-S-2   | 10.774  | LD-S-8                       | 11.692  |                                |         |
| LD-S-18                      | 9.034   | SG-8   | 13.000* | SG-5                         | 16.286  |                                |         |
| SG-15                        | 6.348   | SG-21  | 6.628   | SG-16                        | 11.333  |                                |         |
| SG-19                        | 7.586   | SG-11  | 7.316   | SG-20                        | 8.000*  |                                |         |
| SG-10                        | 6.623   |  |         | SG-17                        | 11.134  |                                |         |
| SG-22                        | 11.091  |  |         | SG-7                         | 6.200   |                                |         |
| FE-1                         | 8.478   |  |         |                              |         |                                |         |
| FE-2                         | 6.000*  |  |         |                              |         |                                |         |
| FE-3                         | 14.500* |  |         |                              |         |                                |         |
| FW-1                         | 5.937   |  |         |                              |         |                                |         |
| FW-3                         | 6.700*  |  |         |                              |         |                                |         |
| WT-X                         | 8.975   |  |         |                              |         |                                |         |
| WT-A5                        | 3.000*  |  |         |                              |         |                                |         |
| Mean                         | 8.848   |  | 11.700  |                              | 12.020  |                                | 15.664  |
| Standard<br>deviation        | 3.416   |  | 4.037   |                              | 4.392   |                                | 4.373   |

environment. By contrast the *Salopina* community is notable for its rich though undiverse fauna. Similar density gradients are observed in modern oceans: Sanders and Hessler (1969) found the abundance of benthonic animals to diminish from 13 000–23 000/m<sup>2</sup> on the shelf edge to about 500/m<sup>2</sup> at the base of the continental slope. This decrease in density reflects the decrease in food supply with increasing depth. The deeper the water column, the less food eventually reaches the bottom owing to scavenging and bacterial degradation during settling, so that deep-sea areas are impoverished in available nutrients (Marshall 1954). We believe food supply to have been the most important single controlling factor of upper Silurian brachiopod distribution.

This hypothesis can be examined by measuring the size of *Isorthis* populations, which tolerated a wide depth range. At any one locality we find gradations between all the *Isorthis* present. Given the low food supply in deep water, individuals should have been unable to reach the same size as those of the same species inhabiting shallow, nutrient-rich waters. The widths of all *Isorthis* brachial valves in all collections were measured. The average width for each collection was then calculated, the collections were grouped into communities and the mean width for each community was



TEXT-FIG. 7. Average size of *Isorthis* in Ludlow communities. Vertical line = average of collection means for each community. Horizontal line = observed range of means. Only one collection in the *Salopina* community.

determined. There is a correlation between community and size of *Isorthis*, the smaller sizes occurring in deep-water communities, and the larger in shallow water (text-fig. 7). The presence in the *Dicoelosia* community of many extremely tiny taxa further supports the food hypothesis. Low food requirements, and hence small adult size, may be strongly selected for in deep environments.

Limited food supply affects the biomass of organisms in the community as a whole. Biomass is determined by both density and size, and these diminish together into the *Dicoelosia* and *Visbyella* communities; size may be particularly important because the volume decreases much faster (as the cube) of the width. The food supply contrast between shallow and deep communities may have been considerable.

#### *Other controlling variables*

While food may determine the lower depth range of a species, the limitations on the upper range are likely to involve the instability of the near-shore region. Shallow-water species are adapted to wide temperature, salinity, and turbidity fluctuations which characterize the shallow, near-shore region. A deep-water species penetrating into the shallows lacks such adaptations and is hence unlikely to survive.

The faunas of this study are benthonic and therefore the substrate is a variable with potentially powerful ecological effects. This is commonly the case in modern faunas (Purdy 1964), but the effects are less profound in lower Palaeozoic brachiopod communities. With the exception of their rocky bottom community, Ziegler, Cocks and Bambach (1968) found little correlation between sediment type and community, and the same is true of this study. The probable reason for this independence is the epifaunal nature of almost all elements of the Silurian communities, as contrasted with the dominantly infaunal modern level bottom associations. As epifaunal filter-feeders, brachiopods are much less dependent on the substrate than animals which live and feed in the sediment.

#### *Ecology of the Visbyella community*

The *Visbyella* community has not been treated in the preceding discussion: it is not yet well known from the Ludlow, and it is discussed by Hancock, Hurst and Fürsich (1974). Some ecological conclusions, however, are given here. The *Visbyella* community probably lived seaward of the *Dicoelosia* community because it appears prior to the *Dicoelosia* community in some shallowing sequences. In addition, graptolites and other pelagic groups are often preserved with the community. The very low population density is consistent with a deep-water environment and follows logically from the *Dicoelosia* community. Extrapolations of rarefaction curves suggest the *Visbyella* community may be much less diverse than the *Dicoelosia* community. Low species diversity might reflect stress conditions on the bottom, such as low oxygen concentrations (Sanders 1969; Rhoads and Morse 1971), but probably means that only a few species were adapted to the conditions of the *Visbyella* community. At the present time, significant diversity reductions take place in lophophorate groups at considerable depth (Jørgensen 1966; Ryland 1970). The *Visbyella* community has some resemblance to the depleted 'Marginal' *Clorinda* community in the Llandovery (Cocks and Rickards 1969), but differs in having its own characteristic species.

### CONCLUSIONS

Using a statistical technique which has taken into account all our collections, this paper has described five major Silurian communities. These are closely comparable to the communities already described in the early Silurian, our *Salopina* community paralleling the *Eocoelia* community, and so on through to the *Visbyella* community, which is equivalent in position to the 'Marginal' *Clorinda* community. All our evidence indicates that these communities are correlated with depth. Their increasing diversity and decreasing density from *Salopina* to *Dicoelosia* agree with the depth-dependent gradients found in modern benthonic assemblages. The *Visbyella* community, with its sparse fauna, probably represents the limit of Silurian benthonic life.

The communities have been shown to reflect an environmental continuum with no natural breaks, and are of the type described by Johnson (1964, p. 107) as 'associations of largely independent species . . . with similar responses to the physical environment'. This is not surprising since the communities are dominated by brachiopods whose ecological requirements as suspension feeders make them more

or less independent of other living animals. Food supply is believed to have been the most important factor controlling their distribution.

In addition to the major communities, we have described several other associations represented by only a few collections. Some of these may result from population explosions of opportunistic species, while others may be assemblages which lived in atypical environments. It is likely that more of these faunas remain to be discovered, but they will be quantitatively much less significant than the main marine communities.

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## APPENDIX

*Localities of collections*

| Area                          | Collection                    | Grid reference | Formation                   |                 |
|-------------------------------|-------------------------------|----------------|-----------------------------|-----------------|
| <b>WENLOCK</b>                |                               |                |                             |                 |
| <i>Salopina community</i>     |                               |                |                             |                 |
| Pembrokeshire                 | FE-3                          | SS 0165.9753   | Silurian of Freshwater East |                 |
|                               | FW-3                          | SS 8840.9940   | Silurian of Freshwater West |                 |
|                               | FW-1                          | SS 8840.9940   | Silurian of Freshwater West |                 |
|                               | 3-doors                       | SM 7622.0827   | Sandstone 'Series'          |                 |
|                               | WT-X                          | SM 7670.0790   | Sandstone 'Series'          |                 |
|                               | WT-A5                         | SM 7626.0828   | Sandstone 'Series'          |                 |
|                               | P-SP-3                        | SM 8628.0876   | Winsle 'Series'             |                 |
|                               | P-W-2                         | SM 8212.0918   | Winsle 'Series'             |                 |
|                               | Sawdde Gorge, Carmarthenshire | LD-S-18        | SN 7221.2507                | 'Upper Wenlock' |
|                               |                               | LD-S-21        | SN 7219.2509                | 'Upper Wenlock' |
|                               | Usk                           | U-P-1          | ST 3480.9990                | Wenlock Shale   |
|                               |                               | *MB 66 (18)    | SO 3355.0096                | Wenlock Shale   |
|                               | East Mendips                  | ND-M-3         | ST 6638.4573                | Wenlock Shale   |
| ND-M-4                        |                               | ST 6632.4576   | Wenlock Shale               |                 |
| †ND-T-1                       |                               | ST 6754.4514   | Wenlock Shale               |                 |
| †ND-AD-1                      |                               | ST 6768.4585   | Wenlock Shale               |                 |
| Tortworth                     | ‡T-W-B                        | ST 6947.9376   | Brinkmarsh Beds             |                 |
| <i>Homoeospira community</i>  |                               |                |                             |                 |
| Pembrokeshire                 | FE-1                          | SS 0165.9753   | Silurian of Freshwater East |                 |
|                               | P-SP-1                        | SM 8626.0874   | Winsle 'Series'             |                 |
|                               | P-W-1                         | SM 8212.0918   | Winsle 'Series'             |                 |
|                               | P-WD-1                        | SM 8332.0931   | Winsle 'Series'             |                 |
|                               | Sawdde Gorge, Carmarthenshire | LD-S-5         | SN 7217.2511                | 'Upper Wenlock' |
| LD-S-4                        |                               | SN 7218.2510   | 'Upper Wenlock'             |                 |
| LD-S-3                        |                               | SN 7218.2510   | 'Upper Wenlock'             |                 |
| LD-S-2                        |                               | SN 7218.2510   | 'Upper Wenlock'             |                 |
| Usk                           | *MB 66 (19)                   | SO 3355.0097   | Wenlock Shale               |                 |
| Tortworth                     | T-BK-1                        | ST 6672.9068   | Brinkmarsh Beds             |                 |
|                               | ‡T-Z-A                        | ST 6672.9068   | Brinkmarsh Beds             |                 |
| <i>Isorthis community</i>     |                               |                |                             |                 |
| Sawdde Gorge, Carmarthenshire | LD-S-16                       | SN 7200.2533   | 'Upper Wenlock'             |                 |
|                               | LD-S-17                       | SN 7204.2527   | 'Upper Wenlock'             |                 |
|                               | LD-S-8                        | SN 7209.2522   | 'Upper Wenlock'             |                 |
|                               | LD-S-12                       | SN 7213.2520   | 'Upper Wenlock'             |                 |
| Usk                           | U-C-1                         | SO 3331.0160   | Basal Elton Beds            |                 |
|                               | *MB 66 (30)                   | SO 3367.0111   | Wenlock Shale               |                 |
| East Mendips                  | ND-M-1                        | ST 6646.4570   | Wenlock Shale               |                 |
|                               | †ND-RL-2                      | ST 6647.4569   | Wenlock Shale               |                 |
| <i>Dicoelosia community</i>   |                               |                |                             |                 |
| Sawdde Gorge, Carmarthenshire | LD-S-14                       | SN 7173.2563   | 'Lower Wenlock'             |                 |
|                               | LD-S-11                       | SN 7182.2553   | 'Lower Wenlock'             |                 |
|                               | LD-S-15                       | SN 7192.2542   | 'Upper Wenlock'             |                 |
| Usk                           | *MB 66 (32)                   | SO 3372.0116   | Wenlock Shale               |                 |

| Area                             | Collection | Grid reference | Formation              |
|----------------------------------|------------|----------------|------------------------|
| Wenlock Edge                     | §P.R.C.I   | SO 5805.9740   | Tickwood Beds          |
|                                  | WE-H-1     | SJ 5924.0045   | Buildwas Beds          |
|                                  | *MB 4      | SJ 6435.0445   | Buildwas Beds          |
| Woolhope                         | W-B-1      | SO 6180.3568   | Wenlock Shale          |
|                                  | W-N-1      | SO 5817.3525   | Wenlock Shale          |
| <i>Visbyella community</i>       |            |                |                        |
| Presteigne                       | PS-N-1     | SO 3045.6245   | Wenlock mudstones      |
|                                  | PS-D-1     | SO 2439.5782   | Wenlock mudstones      |
| Ludlow                           | §B.L.II    | SO 4425.7253   | Wenlock Limestone      |
| Denbighshire                     | §B.L.I     | SO 4425.7253   | Wenlock Shale          |
|                                  | DB-C-1     | SH 8177.6174   | Upper Mottled Mudstone |
| <i>Resserella association</i>    |            |                |                        |
| May Hill                         | ‡M-G-B     | SO 7055.2103   | Woolhope Limestone     |
|                                  | ‡M-O-A     | SO 6869.2244   | Woolhope Limestone     |
| Tortworth                        | T-BR-3     | ST 6736.9130   | <i>Pycnactis</i> Band  |
| <i>Bivalve association</i>       |            |                |                        |
| Pembrokeshire                    | WT-3       | SM 7621.0834   | Sandstone 'Series'     |
|                                  | WT-5       | SM 7649.0806   | Sandstone 'Series'     |
| Sawdde Gorge, Carmarthenshire    | LD-S-19    | SN 7220.2508   | 'Upper Wenlock'        |
| Tortworth                        | T-BR-1     | ST 6735.9131   | Brinkmarsh Beds        |
| LUDLOW                           |            |                |                        |
| <i>Salopina community</i>        |            |                |                        |
| Sawdde Gorge, Carmarthenshire    | SG-19      | SN 7263.2477   | Black Cock Beds        |
|                                  | SG-15      | SN 7266.2480   | Black Cock Beds        |
|                                  | SG-22      | SN 7262.2483   | Black Cock Beds        |
|                                  | SG-10      | SN 7253.2482   | Black Cock Beds        |
| Builth Wells                     | BW-4       | SO 0875.4367   | Whitcliffian           |
| Usk                              | Usk 1      | ST 3681.9826   | Leintwardinian         |
| May Hill                         | MH-10      | SO 6930.1866   | Upper Longhope Beds    |
|                                  | MH-6       | SO 6943.1664   | Lower Longhope Beds    |
|                                  | MH-5       | SO 6943.1664   | Lower Longhope Beds    |
| Ludlow                           | Lud 5      | SO 4377.7358   | Whitcliffe Beds        |
|                                  | Lud 6      | SO 4442.7425   | Whitcliffe Beds        |
|                                  | Lud 11     | SO 4975.7244   | Whitcliffe Beds        |
| <i>Sphaerirhynchia community</i> |            |                |                        |
| Sawdde Gorge, Carmarthenshire    | SG-11      | SN 7254.2481   | Black Cock Beds        |
|                                  | SG-21      | SN 7248.2484   | Black Cock Beds        |
|                                  | SG-8       | SN 7245.2485   | Black Cock Beds        |
| Usk                              | Usk 5      | SO 3749.0017   | Lower Llanbadoc Beds   |
|                                  | Usk 4      | SO 3757.0007   | Upper Llanbadoc Beds   |

\* Collection in the National Museum of Wales, Cardiff, examined by kind permission of Dr. M. G. Bassett. Locality numbers refer to Bassett's monograph (1970, pp. 7-11).

† Collection (made by S. H. Reynolds) housed in the Geological Survey Museum, kindly made available by Dr. D. E. White, of the Institute of Geological Sciences.

‡ Collection data provided by Dr. A. M. Ziegler.

§ Collection made by Mr. J. M. Hurst, Oxford.

| Area                               | Collection | Grid reference | Formation                |
|------------------------------------|------------|----------------|--------------------------|
| Woolhope                           | WH-1       | SO 5950.3987   | Lower Perton Beds        |
| May Hill                           | MH-8       | SO 6944.1664   | Blaisdon Beds            |
|                                    | MH-3       | SO 6944.1663   | Blaisdon Beds            |
|                                    | MH-4       | SO 6944.1663   | Blaisdon Beds            |
| <i>Isorthis community</i>          |            |                |                          |
| Sawdde Gorge, Carmarthenshire      | SG-16      | SN 7243.2489   | Black Cock Beds          |
|                                    | SG-7       | SN 7242.2489   | Black Cock Beds          |
|                                    | SG-17      | SN 7240.2490   | Black Cock Beds          |
|                                    | SG-20      | SN 7234.2494   | Black Cock Beds          |
|                                    | SG-4       | SN 7232.2496   | Black Cock Beds          |
| Usk                                | Usk 3      | ST 3517.9777   | Upper Forest Beds        |
| Ludlow                             | Lud 1      | SO 4289.7296   | Bringewood Beds          |
|                                    | Lud 2      | SO 4296.7312   | Leintwardine Beds        |
|                                    | Lud 7      | SO 4953.7255   | Leintwardine Beds        |
|                                    | Lud 8      | SO 4968.7245   | Leintwardine Beds        |
| Wenlock Edge                       | EH-1       | SO 5705.9500   | Lower Elton Beds         |
|                                    | EH-2       | SO 5737.9425   | Lower Bringewood Beds    |
|                                    | EH-3       | SO 5737.9425   | Upper Bringewood Beds    |
| Denbighshire                       | GB-9       | SH 8625.6226   | Elwy Group               |
| <i>Dicoelosia community</i>        |            |                |                          |
| Sawdde Gorge, Carmarthenshire      | SG-1       | SN 7228.2499   | Tresglen Beds            |
|                                    | SG-5       | SN 7237.2492   | Tresglen Beds            |
| Usk                                | Usk 2      | ST 3650.9827   | Lower Forest Beds        |
| May Hill                           | MH-1       | SO 6950.1649   | Lower Flaxley Beds       |
|                                    | MH-9       | SO 6944.1859   | Upper Flaxley Beds       |
| Malverns                           | §C.W.III   | SO 7605.4413   | Elton Beds               |
| Ludlow                             | 69-A       | SO 4389.7278   | Lower Elton Beds         |
|                                    | LEB 3rd    | SO 4348.7262   | Lower Elton Beds         |
| Woolhope                           | W-N-2      | SO 5815.3516   | Lower Wooton Beds        |
| <i>Visbyella community</i>         |            |                |                          |
| Ludlow                             | 3-NFG      | SO 4337.7263   | Middle Elton Beds        |
| <i>Dayia association</i>           |            |                |                          |
| Builth Wells                       | BW-1       | SO 0550.4890   | <i>Oriostoma</i> Beds    |
|                                    | BW-2       | SO 0930.4670   | <i>Lingula lata</i> Beds |
|                                    | BW-3       | SO 0677.4776   | <i>Lingula lata</i> Beds |
| Ludlow                             | Lud 3      | SO 4311.7314   | Leintwardine Beds        |
|                                    | Lud 4      | SO 4318.7314   | Leintwardine Beds        |
| <i>Gypidula/Atrypa association</i> |            |                |                          |
| Sawdde Gorge, Carmarthenshire      | LD-S-1     | SN 7225.2503   | 'Upper Wenlock'          |
| Usk                                | Usk 6      | SO 3747.0019   | Lower Llanbadoc Beds     |
| Ludlow                             | Lud 10     | SO 4934.7263   | Upper Bringewood Beds    |
| <i>Lingula fauna</i>               |            |                |                          |
| May Hill                           | MH-11      | SO 6908.1907   | Clifford's Mesne Beds    |

§ Collection made by Mr. J. M. Hurst, Oxford.